FUNGI, FRIENDS AND FOES

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FUNGI, FRIENDS AND FOES

by A. F. Parker-Rhodes

PAUL ELEK

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CHAPTER I

BURIAL OF THE DEAD

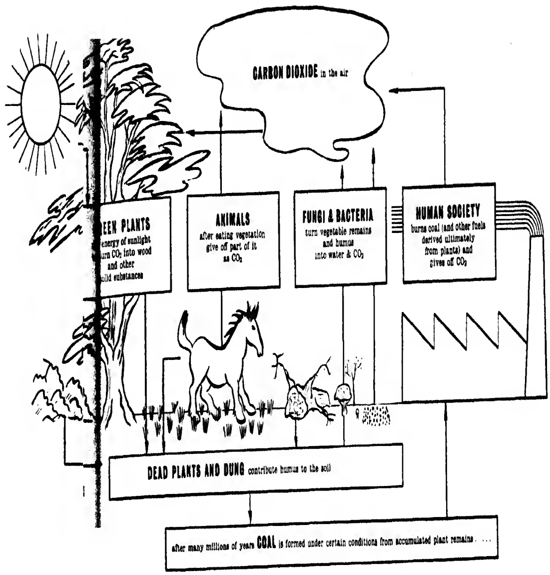
ALL organisms die, except those that are so small as to be able to divide their whole bodies into two new ones; apart from these the death of the individual is necessary to the survival of the race. Consider how difficult it would be to find food enough for all the human beings in the world, if they lived to see, say, ten generations, instead of only two as they in fact do. Obviously for any animal, which has to eat, immortality is out of the question; but plants are able to make their own food out of ingredients universally present in the air and the soil, using for this purpose the energy of sunlight. We might suppose therefore that they could manage to "live for ever" without imposing too geat a strain on the world's resources; there is plenty of carbon dioxide in the air, which is their main requirement, for many more plants than actually exist in the world. As a matter of fact, trees do not have any special features in their life history which foredoom them to death, as animals and annual plants have; they do not grow old. But all the same they do not in fact continue for ever, and every one sooner or later meets with a fatal accident. In the larger trees this usually consists in the trunk being eaten away by insects until it is no longer strong enough to support the weight, and the tree falls.

Such fatal accidents do not, however, afford a final solution of the problem. The fallen tree is to a large extent made up of materials derived from carbon dioxide, and if it lay there, just as it fell, for ever, that much carbon would be locked up in a form useless for the surviving plants. With the passing of ages the whole supply of carbon dioxide in the atmosphere would be used up, and all the plants would

die. And all the animals too, for they all depend directly or indirectly on plant life. But long before that the forest regions of the earth would present a very odd appearance: there would be a tangle of trunks hundreds of feet deep, through which the young trees would have to make their way upward to the sun.

Why does all this not happen? It is because the dead trees do not lie there, just as they fall, but in the course of time decay and rot away and mingle with the soil. We are so familiar with this idea—everything in time decays and rots—that we are apt not to wonder why it happens. It used to be thought that organic materials like wood were unable to hold together without being part of living organisms, but if left to themselves would decompose, just as the photographer's "hypo" decomposes if left exposed to the air; but chemists have now investigated wood pretty thoroughly, and the older "heart-wood" which makes up the greater part of the trunk, at least, is a very stable substance, and needs such powerful agents as sulphuric acid to decompose it in the laboratory. So we cannot put down its decay to "spontaneous causes"; we have to find out what *makes* wood decay. The insects which eat out the heart of the living tree, or others like them, certainly do something towards finishing the job they have begun, but they cannot do it all, for a large part of the wood is indigestible to them. We have to look further.

The answer turns out to be that the main buriers of the dead, at least of the vegetable dead, are toadstools, or more accurately fungi of which toadstools are one of many kinds. These organisms are endued with the power to change cellulose and a great many other things of which living and dead plants are composed, into water and carbon dioxide,



I. THE CARBON CYCLE

Note that apart from human intervention the fungi and bacteria are the only agents returning the carbon in humus and vegetable remains to the air in appreciable quantity.

and smaller quantities of ammonia and mineral salts. They leave behind a fine dark brown powder which forms one of the main constituents of the soil; this is itself decomposed by other fungi, though at this stage in the process bacteria, which are very much smaller kind of organism, play a larger part. These bacteria start work at the same time as the fungi, but to begin with are less important. It is they too who dispose of the fungi when they die. Bacteria themselves are too small to need an undertaker and those that do not divide to perpetuate the species get eaten by the little animals that live among decaying vegetation, or else do decay of themselves. There is thus a kind of universal balance between the using up of carbon dioxide by the plants, and its restoration, mainly by the action of fungi. This is illustrated in fig. 1; it is called the carbon cycle.

We have mentioned the role of fungi in getting rid of trees when they are dead, but there are other kinds that can attack trees and other plants while living, of which we shall have much more to say in later chapters; they are called parasites (in contrast with saprophytes, which can only live on dead organic matter), and they help the insects in weakening the tree and preparing it for its "fatal accident". Some can only attack a plant that has been injured, as by the loss of a bough or twig, while others can get a foothold even on uninjured trees; nor are they limited to the woody parts, for many specialize in attacking the leaves, or the green stems of herbaceous plants. Then again there are root-parasites, and a variety of saprophytic forms which dispose of the year's accumulation of dead leaves on the forest floor. Outside the plant kingdom there are fungi which live on animals or other fungi, but in these roles they are much less important than bacteria and one-celled animals.

Thus we see that these organisms called fungi, of which the most familiar are the toadstools and mushrooms, are very essential in the economy of nature; it is no exaggeration to say that without them life could not exist on the earth because of the accumulation of dead plant material which would follow. Early in their history these organisms, whose original role was that of forest sextons, took to burying the living as well as the dead, and, as parasites, are the cause of the greater part of the diseases which afflict our cultivated crops, and a few which affect ourselves. In this book it may seem that we have more to say about the damage that fungi do than about the good we get from them. But the chief service they perform is what they do in the state of nature and it is only when man starts to change the course of nature to his own benefit, by growing great fields of tall grasses of a kind unable to survive in the natural state, or making artificial forests of fruit trees, that it becomes difficult to restore the balance thus upset, and good farming consists

essentially in providing by conscious care what is achieved in nature as a result of the inevitable balance of random forces; for this purpose the farmer employs various unnatural expedients such as the use of fungicides, about which we shall have more to say later on.

Apart from their function as disposers of dead plants, fungi have been put to a variety of useful purposes by man, as manufacturers of chemical (particularly medicinal) substances, and as food. But before going into these matters in detail, it will be necessary to describe what manner of organisms these fungi are, how they live, and what they do.

CHAPTER II

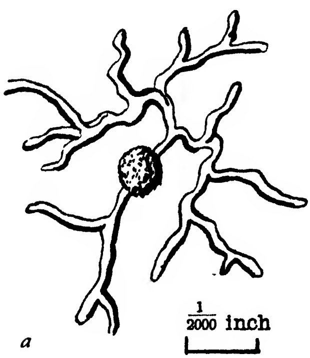
FAIRY RINGS

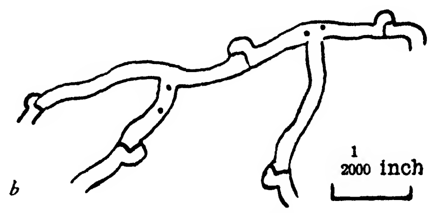
In the last chapter we drew attention to the problem of what happens to trees when they die and fall down; the same problems arise, though less strikingly, with the grass and clover which make up our pasture fields. The rate of accumulation of dead matter is smaller than in the woods, but it has to be got rid of just the same, and here also the fungi are the main agents responsible. Let us then watch some of them at work, because it is easier to discern what happens here, than in the tangled undergrowth of the woods.

Most country people are familiar with what are called "fairy rings"; they are circular rings of grass deeper green in colour than the rest of the field, which are especially conspicuous in the summer; they can however be made out at all times of the year. All sorts of stories have been told to account for them, beside the well known one that they mark the places where the fairies are accustomed to dance. Among the more naturalistic explanations put forward were that they were caused by the urine of cattle, or that they were produced where a lightning-flash struck the ground. Actually of course they are the visible sign of the growth of fungi; and since their behaviour illustrates many points in the behaviour and life history of fungi, I shall spend some time in describing them.

One of the commonest field toadstools in this country is *Marasmius oreades*, known in some parts as the fairy ring mushroom on account of its conspicuous ring-forming habit. The fungi themselves are small and of a pale brown colour, moist, but not slimy, to the touch, and having rather thick "gills" underneath the pileus (the hat-like part of the toad-

stool). They come up from June to September, or even later, nearly always in grassland. Fig. 3 shows diagrammatically three stages in the early life of one of these rings. In 3*a* is shown the ring in its first year; C marks the spot where the spore fell. All fungi are reproduced from spores, which are of many different kinds, those of this species being among the simplest in structure; they are little oval transparent bodies not more than a 5000th of an inch long, consisting of a single cell enclosed in a thin transparent case. If such a spore finds itself in a favourable spot (and it is millions to one against this, so that the fungus has to produce millions of spores to keep the species from extinction), it puts out a little narrow tube with a thin wall (made of the same kind of substance as an insect's hard skin, but far thinner) which may be less than a 10,000th of an inch in diameter. Presently, if conditions remain favourable, it will branch, and branch again, all the time drawing nutriment from the humus and other organic matter which it finds in the soil, and also, in the present case, grass roots. In a week





2. HYPHAE

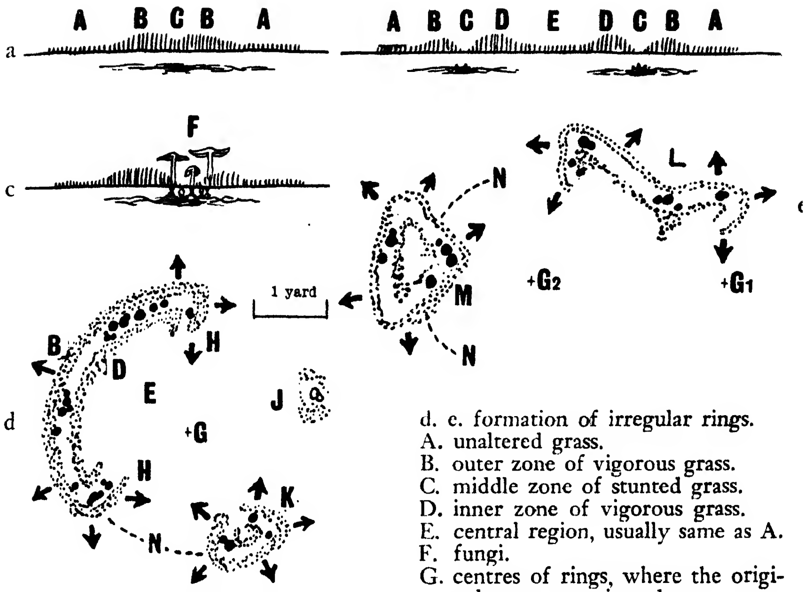
a. spore of Russula germinating, general view

b. mature hyphae of binucleate mycelium, showing paired nuclei and clamp-connections. Diagrammatic.

or so the young fungus takes the form of a weft of fine threads, called the mycelium, forming a circular patch a few inches across under the soil, as shown in diagram 3*a*. After a time the grass above it is stimulated to a more vigorous

growth, probably because the fungus excretes into the soil compounds of ammonia which act as a local fertilizer in the same way as the sulphate of ammonia used by the farmer. But it may be that the action of the fungus is more complicated than this.

Anyway, the beneficial effect is short lived, because when the mycelium becomes well established it retards the growth of the plants around it, probably by noxious secretions, and thus there appears a central patch of stunted vegetation, marking the oldest part of the mycelium (at C), surrounded by a green belt where the fungus threads, which are called hyphae, have recently penetrated. This zone is marked B, while A represents the unaltered grass around the patch. This is as far as the fungus gets in its first year, but early next summer (the growth of fungi, being dependent on that of plants, comes later in the year than theirs) it resumes growth, and a third zone appears. For when it has been growing some time in one place, its noxious products accumulate (plants do not produce such noxious excretions, but animals do so), and since it cannot go away as animals can the central and oldest part of the mycelium dies; the ground where it grew cannot for some time be reoccupied by the fungus, and thus, being compelled to grow always outwards, a gradually widening ring is formed. Where the hyphae have poisoned themselves and died, their remains once again act as manure to the grasses, and an inner green zone fig. 3*b*, D) and inside that a zone E which usually resembles in appearance the outer unaltered grass at A. The toadstools themselves are produced usually in the middle dead zone C, where the mycelium is most vigorous. Unlike animals but like trees, fairy rings seem never to grow old, but unlike trees the chances of a fatal accident happening to them get less as they get bigger, and thus they may reach great ages. Some rings in America have been judged by their size and yearly rate of growth to be about 600 years old,



3. FAIRY RINGS

a. diagrammatic view at end of first year's growth.
b. diagrammatic view at end of second year's growth.
c. section of one side of ring bearing toadstools.
d. *e.* formation of irregular rings.

d. e. formation of irregular rings.
A. unaltered grass.
B. outer zone of vigorous grass.
C. middle zone of stunted grass.
D. inner zone of vigorous grass.
E. central region, usually same as A.
F. fungi.
G. centres of rings, where the original spore germinated.
H. "horns" formed by growth of rings at broken ends.
J. isolated fragment of a ring.
K. re-formation of a complete ring
L. M. formation of irregular patterns by combination of factors.
N. circumference of original ring at time of breakage.

but older ones are usually too much broken up to be distinguishable as rings. Some typical fairy rings formed by *Marasmius oreades* are shown in fig. 4, p. 16.

People usually imagine mushrooms and toadstools as "coming up in the night", but this is not quite a true picture. The last part of the development, from being small knobs hidden in the grass to conspicuous toadstools, may take only a few days (see for example fig. 5, pp. 18/19, which shows a particularly rapidly growing species), but from its first beginnings recognizable under the microscope the life of a fairy-ring toadstool may be many weeks. These first beginnings are usually laid down in the spring, through a

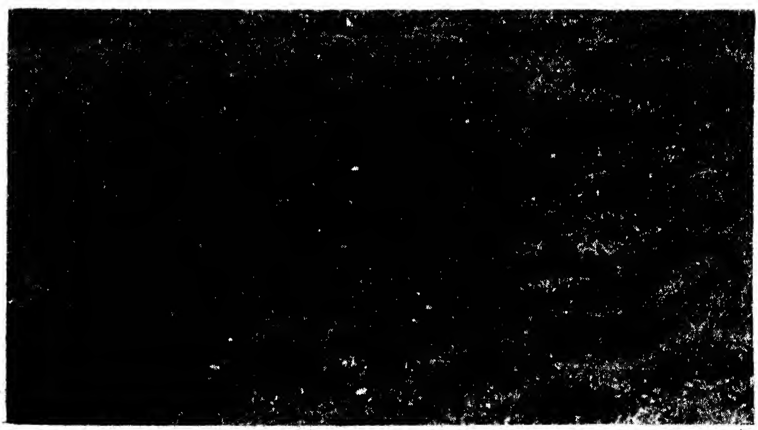
group of hyphae coming together into a small knot, less than a pin's head in size. These knots grow only slowly, until conditions become favourable for further development; we do not yet know what these conditions are; for though there may be many rings side by side in one field, some will be decorated with a fine crop of toadstools, while others will remain barren, only to fructify later in the year when the first has finished. No doubt temperature and soil moisture have something to do with it, but the question remains one for future investigators to unravel.

It may be asked why, if this account is correct, are the kinds of fungi which sometimes form rings not invariably so arranged; one part of the answer is illustrated in fig. 3, *d* and *e*. When, (through being uprooted, as by cattle, or otherwise destroyed in part of its circumference), a ring is broken, its pieces will grow round at the edges, not only outwards as before, but sideways, though still not into the unwholesome inner region; in this way it acquires, in the following year, "horns", as at H in fig. 3*d*. After a few years when the inner region has lost its toxicity these horns may join up to form a new, but now irregular, ring, as at K or M. A small fragment such as J may grow out as if it were a first year's ring, and form a regular circle. A second cause of irregularity is the meeting of two rings; in such a case the mycelium where they meet can grow neither one way or the other, since in both directions lies poisoned ground, so that it dies, and an hour-glass-shaped ring results. The combination of these two factors may produce all sorts of shapes, as in fig. 3*e* which would not be recognized as fairy rings at all by most people.

Let us now look more closely at the structure of the fungus itself. We have already seen how the mycelium, from which the toadstool is produced, is made up of microscopic threads, the hyphae. The visible part of the fungus is made up of very similar threads, closely interwoven to form a

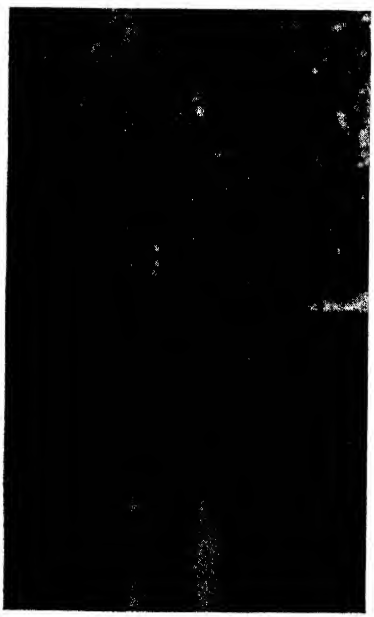
4. MARASMIUS OREADES

a. close up view of the toadstools.
b. fairy-rings caused by *M. oreades* at Pentireglaze, N. Cornwall. The largest of these rings is 44yds in diameter, and may be 100 yrs old.
c. an unusual ring marked by a growth of ragwort, with the interior of the ring differing in vegetation from the outside.



10 a.m. First Day

6 p.m. First Day



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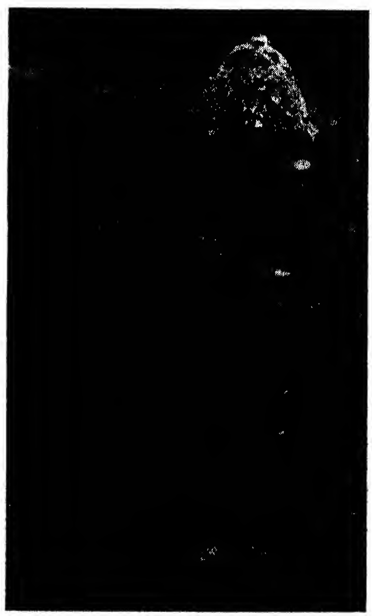

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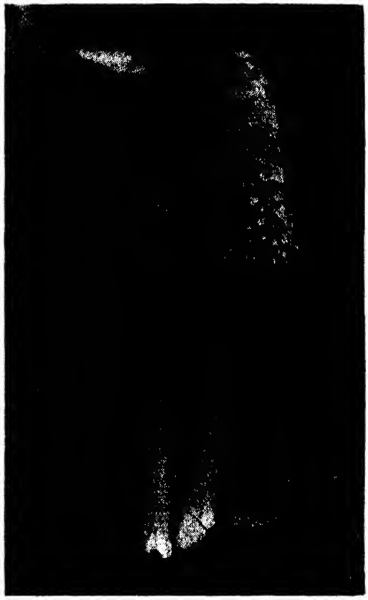

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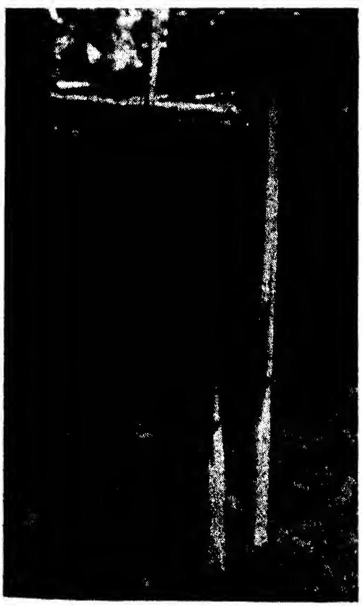
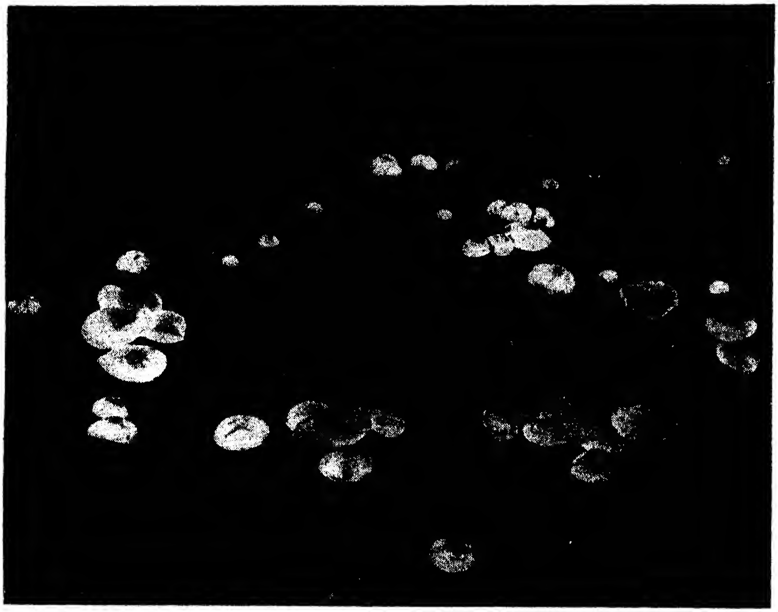


10 a.m. Fourth Day

5. SEVEN STAGES IN THE DEVELOPMENT OF A TOADSTOOL,

COPRIMUS COMATUS. In this toadstool spore--dispersal is facilitated by the pileus and gills decomposing into an inky fluid when the first spores have been shed from the lower end of the gills, so that there is nothing to stop the spores formed higher up on the gills from falling freely to earth. The photographs were taken alternately at 10 a.m. (first and last pictures) and 6 p.m. BST.



8. A MIXED FAIRY-RING. The conspicuous white fungi are *Collybia maculata*, and the smaller dark ones are *Lactarius rufus*. The two rings do not quite coincide.

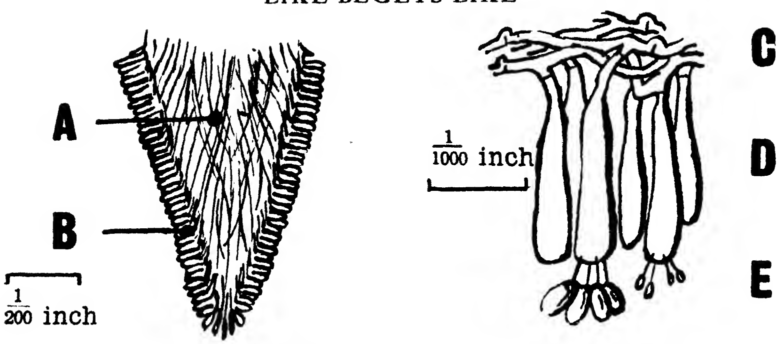
middle part of the mycelium takes a long time to die away, as with *Hygrophorus virgineus*, a common little white toadstool. With the common mushroom, and many other species having a preference for dung or very rich soil, no ring is formed because the mycelium only grows well in special patches, as where dung has lain. Another complication of the ring forming habit is that if the rings of two *different* species meet, it often happens that their poisonous products have no effect no each other, so that they can intersect, which two rings of the same species cannot do. Fig. 8 shows a mixed ring formed by *Collybia maculata* (whitish) and *Lactarius rufus* (dark); the two rings do not quite coincide, but that is hard to make out from the photograph; they could not of course be made out as rings if the toadsools were not there, because they are in a wood.

CHAPTER III

LIKE BEGETS LIKE

LIKE all other organisms, fungi are able to "breed true", that is to say, they always grow from spores produced on fungi like themselves in all or nearly all essential characters, and the spores from one fungus never (or almost never) grow into anything but another fungus of the same kind; even when one does occasionally get a "sport" or aberrant type, the difference between it and its parent concerns only one peculiarity, and does not amount to its being of a quite different species. Of recent years we have learnt quite a lot about how this effect is achieved, not only in fungi but in animals and plants, for it turns out that the machinery by which the characteristics of different species are regularly and exactly transmitted to their descendants are very much alike in all living things, except perhaps the very smallest. In this chapter we shall give a very condensed account of these matters as they affect the fungi.

There are two kinds of spores produced by fungi, called perfect and imperfect, which terms date from the time when people still tried to interpret natural history by human standards. The perfect spores are in the toadstools produced on the gills under the pileus; they are formed on special cells which are packed close together side by side on the surface of the gill, called basidia (see fig. 9, p. 24), and each basidium bears four spores (sometimes other numbers, such as two in some kinds of mushroom) on the end of minute pointed stalks. Just before the spore is ready to be discharged, each stalk produces a little drop of water about as big as the spore, and then there follows a miniature explosion, which carries the spore up to a hundredth of an inch out from the gill



9. SPORE-BEARING ORGANS OF TOADSTOOLS
a. section of gill. *b.* part of hymenium, showing basidia and spores.
A. trama, or central supporting tissue.
B. hymenium, or fertile layer.
C. subhymenium.
D. basidia and "cystidioles" or sterile basidia.
E. spores.

surface. After that it falls straight down till it gets clear of the shelter of the pileus, when the least current of air may waft it, because it is so small and light, for great distances. In other kinds of fungi than the Basidio mycetes, in which the toadstools are classified because they have basidia, the perfect spores are formed in different ways, which we shall describe later on; what makes them all "perfect" spores is this: that immediately before they are formed the basidium, or other organ which produces them, has two nuclei which flow together into one. Every cell of every organism (except dead cells) has one or more of these nuclei, whose presence is essential to the life of the cell, and which are responsible for the complete organism developing into the adult form characteristic of its species. It is believed that every character of the species is determined in the course of development by the action of particular ultramicroscopic bodies called genes, of which there are tens of thousands in every nucleus; every nucleus carries one of each kind of gene, although each one takes effect only in those parts of the fungus which it is its province to regulate.

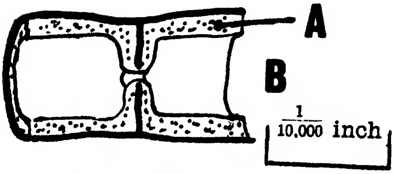
According to this mechanism every nucleus throughout the fungus ought to have the same set of genes, and this is

achieved by a very complicated process which goes on every time a nucleus divides into two, the purpose of which is to ensure that each separate gene shall first divide into two identical daughter-genes, and that one shall then be given to each of the daughter-nuclei. Normally the division of the nucleus is a necessary prelude to division of the cell. In the basidiomycetes it is not true that every nucleus carries an identical set of genes, because most of the cells (in a fully adult fungus all of them) possess two nuclei, each of which carries a different set; but the *cells* nevertheless have all the same set or rather pair of sets. Now according to what has been said, it would be supposed that different sets of genes would mean different kinds of toadstool; so it does, but in nature the differences are quite small ones, not sufficient for separating the individuals into different species. It is well known that mushrooms are not all alike, some being larger, other having thicker stems, others having different shades of colour, and so on; it is these quite minor differences that are concerned, when we speak of the gene-sets of fungi of one species being different. Nevertheless, though the differences are so small, they are the raw material on which evolution works, and by their accumulation over ages new species are eventually formed, if the particular selection of characters concerned is one having an advantage in the struggle for reproduction.

When the two nuclei fuse in the cell which is destined to produce the "perfect" spores, their gene sets get to some extent shuffled together and in the two divisions of the nucleus next following, they are again sorted out into single sets, one to each of the four daughter nuclei. But because of this shuffling the four resultant sets are not all alike and thus the four spores when they germinate will produce four very slightly different types of toadstool; it is this variability in the offspring which is the purpose of the perfect spore forms. In contrast to this process is that by which the *im-*

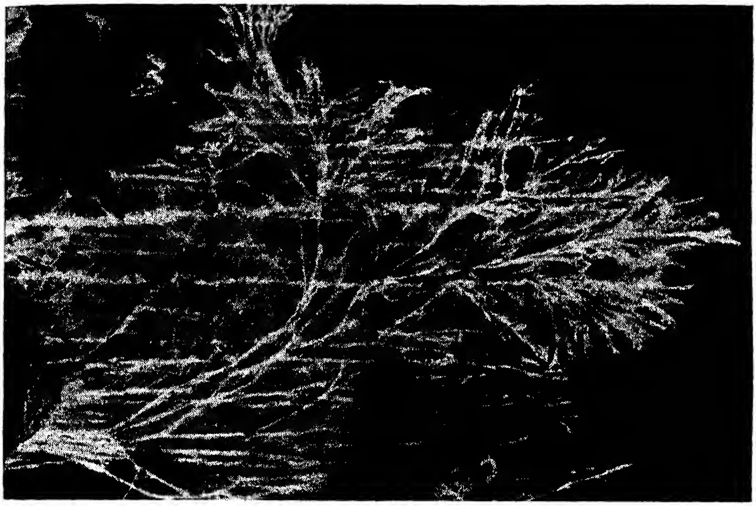
perfect spores are produced, in which a nucleus is simply separated off from its cell into the young developing spore without any fusion of nuclei having taken place. Thus every imperfect spore from a given individual will give rise to an identically similar one (unless there are two types of nuclei present, in which case there will be two daughter types possible instead of the infinite variety possible with perfect spores).

We now have to explain how it happens that there come to be two different kinds of nuclei in the basidium and in other cells of the fungus, seeing that their perfect spores have only one. In animals and plants this is typically brought about by sexual union and by pollination though in these cases, unlike fungi, the nuclei flow together as soon as the sexual cells have joined, and thereafter divide so as to distribute the double gene set equally to the daughter nuclei, and only deal out single sets again when the next generation of sexual cells come to be formed. Fungi have never learnt to divide double sets of genes in this way (this may not be true of the yeasts), and instead they have the arrangement of pairs of nuclei in their cells as described above. This gives them one great advantage, which we shall now explain. After the mycelium has begun to branch and spread out, two hyphae which meet one another (in the region where the cross-walls have not yet appeared) may join together, the intervening wall being dissolved away, so that the mycelium becomes a true network. The hyphae, when fully mature, have the living substance or "protoplasm" confined to the outer region just inside the containing wall, as shown in fig. 10, A; B in this figure represents the watery



10. STRUCTURE OF A FUNGUS HYPHA. Note the perforation in the crosswall.

A. Protoplasm, forming a layer round the edge. B. Central vacuole.



11. MYCELIUM
This picture of the mycelium of one of the Corticiacei (a lowly family of Basidiomycetes), growing on a rotten log, gives a good idea of its appearance.
Photo. Mustograph.

juice which fills the centre. When two hyphae have joined together as described the central regions also join, so as to form the same structure as does a single hypha cell which has branched. Now just the same thing can happen if two different mycelia of the same species come into contact, but in this case there is a sequel. The immediate result of fusion is the formation of a cell having two different kinds of nuclei in it, each nucleus may then divide, and one of its daughters pass through the pore in the cross-wall into the neighbouring cell where there is a single nucleus of the other kind; there it divides again and one passes on to the next cell. The same sequence of events meanwhile takes place in the other mycelium, and the final result is that there is produced a pair of mycelia each having two nuclei in each cell; they are then called binucleate (as opposed to uninucleate). In most toadstools and probably other fungi as well it is not possible for *any* two mycelia to take part in this process of

"diploidization"; usually there are two "sexes"; such that only mycelia of opposite "sex" can diploidize each other. But unlike the sexes of animals and plants, there is no outward difference between them, and furthermore there may be more than two. In such cases it is only certain combinations that are fertile, others being unable to diploidize each other; e.g. we might have A-B, A-C, B-D, and C-D as fertile combinations, but not A-D or B-C.

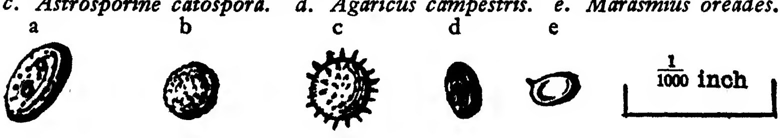
Some fungi, although normally requiring diploidization before they can produce perfect spores (most toadstools in this category will not produce anything beyond the mycelium unless they are diploidized), can go through the motions of producing perfect spores while still in the uninucleate stage; in that case the spores produced although outwardly of the "perfect" form are, like imperfect spores, all alike. A few species will produce toadstools when uninucleate, but without spores on the gills, or else toadstools of half the normal size.

The disadvantage of this process is that it depends on the chance that suitably related mycelia will meet. Some fungi such as those which cause rust of wheat described in Chapter IX have elaborate arrangements to improve their chances in this respect, but the usual method is to produce large numbers of imperfect spores, which can be done without so much trouble and which in effect disseminate one and the same mycelium over a very wide area. For this reason the imperfect spores, of fungi which have them, are produced usually in much greater numbers than the perfect forms; indeed a large number of fungi belonging to the Ascomycetes, a group which do not have their spores on basidia like those of toadstools, have taken to doing without the perfect stage altogether. These are called imperfect fungi, and are a great trouble in classification because it is only by a study of the perfect spore producing stage of the fungus that a satisfactory classification can be made out. Many others of

these Ascomycetes, perhaps a majority, have adopted the practice of self-diploidization, which has the same effect. In such cases the species sacrifices variability, and ability to adapt itself quickly to changed circumstances (by the survival of some at least out of the innumerable types in existence) to the immediate gain of very rapid multiplication.

The number of spores produced by fungi is indeed vast. Spores (mostly imperfect forms, of the thin walled and short lived type called conidia) are found in the air even up to 20,000 ft and over the great oceans. For this reason they are mostly of very wide distribution. Unless limited by temperature requirements to tropical or temperate latitudes, or parasitic on some particular species of plant, most species are in fact found throughout the world. Fungi other than Basidiomycetes cannot effect diploidization quite so readily as described above; as will be realized from our description the process can occur at any age in the life of the mycellium. Thus it is easier for the Basidiomycetes to produce adequate numbers of perfect spores, and very few of them do in fact find it necessary to have imperfect forms at all. Thus they have evolved in the direction of producing their perfect spores ever more abundantly. The fairy-ring toadstool, a relatively primitive type, may bear tens of millions of spores; the most advanced toadstools such as the dung-inhabiting *Coprinus* may reach to milliards, while the record is held by the giant puffball (*Calvatia gigantea*) a good specimen of which may contain several billions of spores. Fig. 12 illustrates some of the variety of spore form found among toadstools; not only do they differ in shape, but in colour, and this is one of the main guides to identifying the different kinds.

12. TYPICAL SPORE FORMS OF TOADSTOOLS
a. Laccaria laccata v. *proxima.* *b. Russula atropurpurea.*
c. Astrosporine catospora. *d. Agaricus campestris.* *e. Marasmius oreades.*



CHAPTER IV

FOREST FUNGI

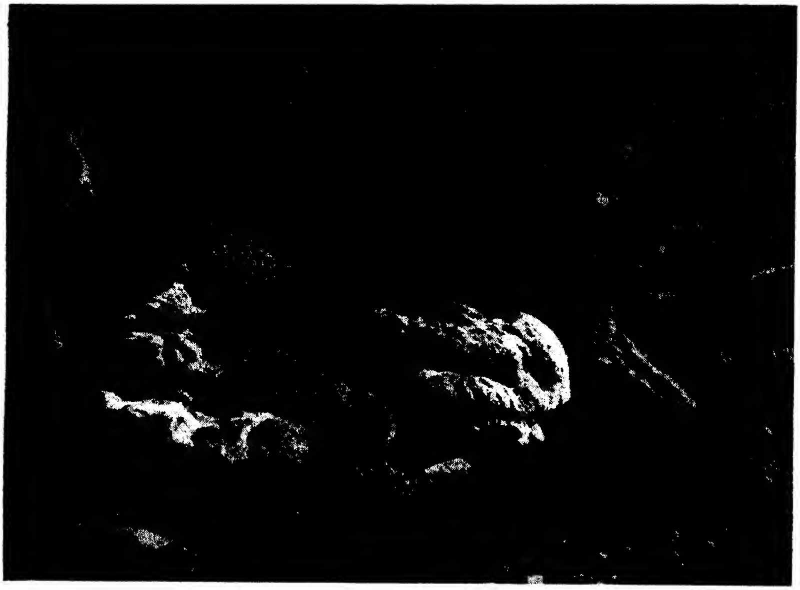
HAVING said something about the life history of the toadstools, which are the most familiar kind of fungi to many people, let us now look at them in their favourite surroundings which are provided not by open pastures but by woods and forests. In Britain we have not got very large tracts of forest land, and rely on other countries for timber and its products; this is a drawback which became apparent during the late war, when for example the paper shortage made everyone aware of the importance of forest trees in the economy of the world. In this chapter we shall try to show how important a part, for both good and ill, fungi play in the management of forests.

It is probable that the so-called "higher" fungi, which term includes the Basidiomycetes (the toadstools, bracket-fungi, and their allies, which produce their spores on basidia such as were described in the last chapter) and the Ascomycetes, which we shall describe later, evolved at about the same time as the higher plants. Unfortunately we cannot check this directly, by examining fossils, because fungi very rarely get fossilized; the evidence for this view is that on the whole the more primitive types of fungi grow among or on the most primitive types of plants, while the types having a more complicated structure are found associated with plants which we know to have appeared most recently; the clearest example being the greater variety of fungus types in deciduous and mixed forest than in coniferous woods. In a typical English oak wood, for example, we can find fungi growing in a very great number of situations: on living trees and undergrowth plants, as parasites; on fallen

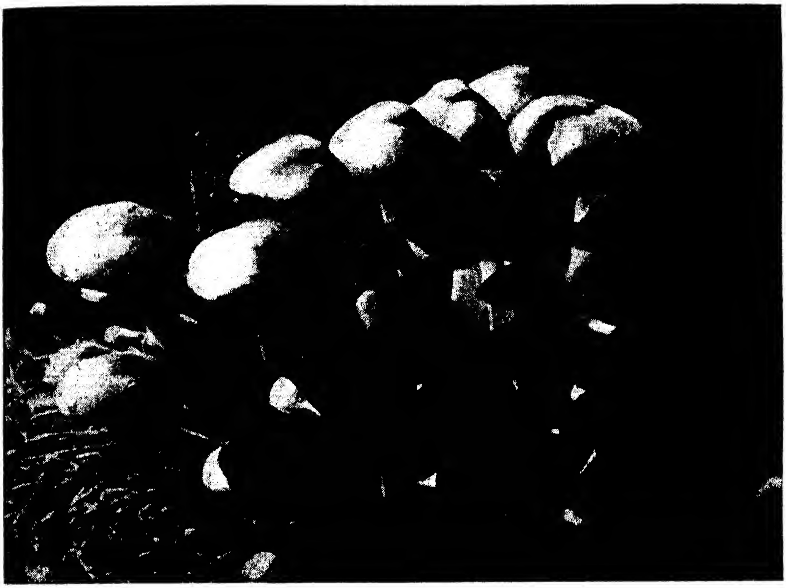
13. BULGARIA INQUINANS
(Ascomycete, of the class Discomycetes).
A parasite of the beech tree, which fructifies after the tree is dead.

trunks in various stages of decay, as saprophytes; on dead leaves, and in the decaying leaf mould; on the bark, under the bark, and in the wood itself; in swampy ground and on dead grasses; nowhere conspicuous, but everywhere active and often in conflict with human purposes, are members of the fungus kingdom. Just because they are adapted to the role of destroyers, being unable to make their own food out of water, carbon dioxide, and mineral salts, as plants can, they are apt to be enemies of man, whose purposes are mainly constructive; thus it happens that our efforts to produce timber for our social needs are much concerned with preventing fungi from fulfilling their natural role in forest life.

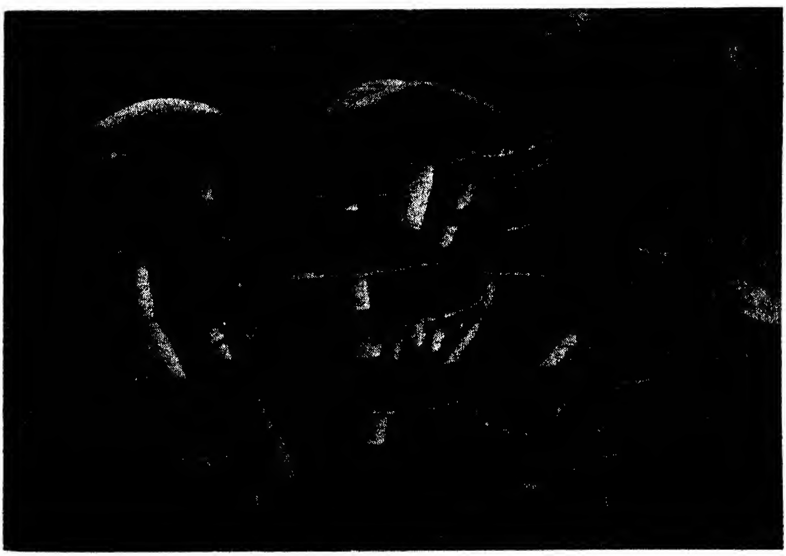
There are three main stages in wood destruction with which fungi are concerned; some species, and these are the

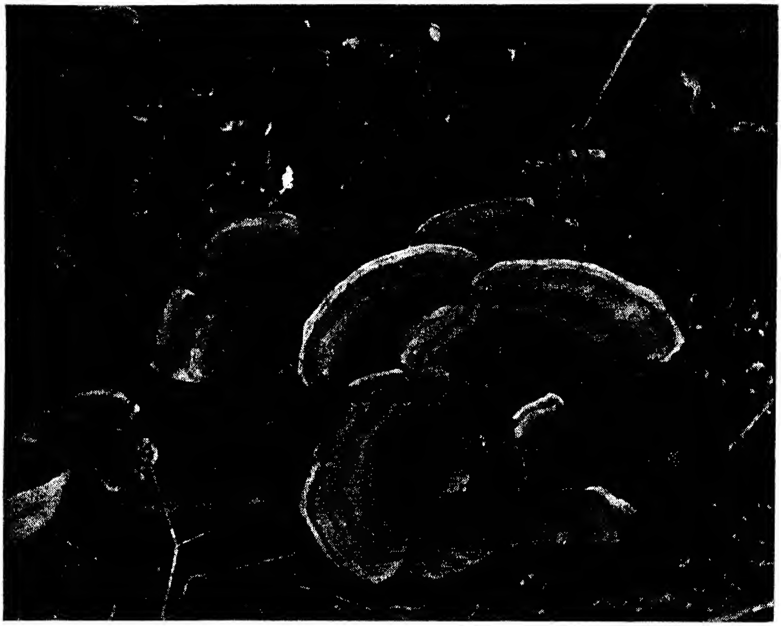


a. Xanthochrous hispidus. Photo. Peter Ray
14. PARASITES WHICH CAUSE MUCH DAMAGE TO TIMBER
b. Polyporus squamosus. Photo. Mustagraph



a. Hypholoma sublateritium on an old stump.
15. WOOD DESTROYERS OF THE SECOND STAGE (non-parasitic).
b. H. appendiculatum. Photo. Peter Ray.

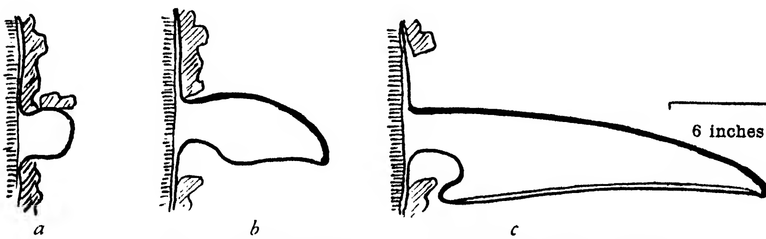




16. POLYSTICTUS VERSICOLOR.
A very common wood-destroyer, which comes in too late to be a serious pest.

most important economically, attack the tree while it is still alive, getting a foothold, either through dead or broken wood, or through the leaves, or by way of the soil into the root system. Next, after the tree is dead, but while the wood is pretty nearly in its living condition, other species, which are not able to act as true parasites, can start work; nearly all the true parasites of economic importance also go on growing during this stage also; often a newly fallen trunk will give a quantity of quite usable timber, but in a short time, if it is left to lie, these second-stage fungi will render it useless. The last stage, which concerns the student of fungi more than the forester, begins when by the action of these fungi the wood has been reduced to a soft pulp or powder; then the work of destruction is completed by a third group of fungi, this time with more liberal assistance

from bacteria. Of course it must not be imagined that the three groups are really sharply distinguished from one another; the classification means more in economic terms than in biological, and different species vary considerably in how closely they are tied to a particular stage in the process. Among those which come in latest are some very primitive types such as *Dacryomyces* (fig. 7, p. 21), and also some advanced ones such as the puff-ball *Lycoperdon pyriforme*. The middle stage is represented by a great variety of types, of which the very common *Stereum hirsutum*, *Polysticus versicolor* (fig. 16), and the edible *Pleurotus cornucopiæ* are examples.



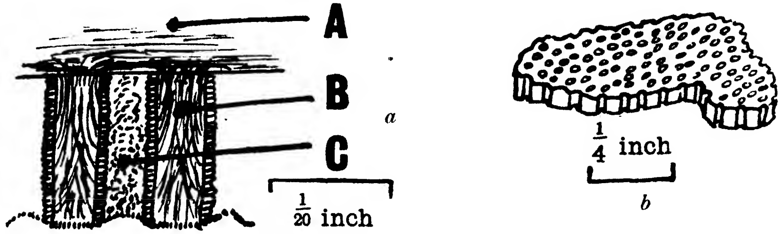
17. DEVELOPMENT OF POLYPORUS BETULINUS.
a. first stage (in section). *b.* appearance of upper and lower surfaces. *c.* mature form.

As an example of the first stage, we shall take *Polyporus betulinus* (fig. 17); this is one of the many true parasites which carry over into the second and even the third stage. This species is extremely common on birch trees; so common indeed that it is probably the immediate cause of death of the majority of sizable trees of this species. One of the innumerable spores which are always available in the air alights on the bark of a healthy tree, and, as soon as a shower of rain falls, begins to germinate in the surface film of moisture. Because it is so very small, its own resources are only sufficient for it to produce a germ-tube, or embryo hypha, less than an inch long; it does not grow very straight, and the chances of its meeting a crack in the bark which it can grow through are small; as soon as the bark dries in the

sun, the little hypha dies. But there are plenty more, and an occasional one may land near to one of those natural crevices in the bark, through which air is admitted to the interior tissues of the tree, and thus be able to gain entry into the living cells of its host, from which alone it can, at this stage, draw its food. It is able to grow between the cells, which is made possible by various chemicals it produces which can destroy part of the cell walls; it thus passes inwards to the wood, and once established it can attack the wood itself, though the cells of this part of the plant are no longer living. Within a year the mycelium of the fungus, which is very similar in structure to that of a pasture toadstool, has grown throughout a large part of the tree. By softening the wood it assists the attack of wood-boring insects, which in turn by making holes make easier the entry of other fungi, including those that are not able to attack the living cells directly; finally, by making the wood unfit for its proper function of carrying water from the roots to the leaves, it will kill the tree by its own efforts, if the insects have not already felled it.

So long as the tree remains alive, which may be many years if it was well grown when first attacked, there is usually no visible outward sign of the presence of the fungus; but when it, or a part of it, dies, the fungus begins to form its spore bearing structures. This is quite a common habit, for there are many fungi which attack living trees, but remain in a state of arrested development until the tree is dead. In the case of our *Polyporus*, the adult stage first appears as a hemispherical knob just below the surface of the bark (fig. 17*a*); this remains almost in its original shape until it is a few inches across, and then (if it has not been destroyed by insects which specialize in this form of food), begins to flatten out underneath (fig. 17*b*); eventually it forms an expanded hoof-shaped structure up to eighteen inches across and four inches thick, soft to the touch, and

covered with a tough grey upper layer but pure white underneath. The lower surface has a layer of tissue, while actively growing, up to ¼″ thick, which can be peeled off; if it is held up to the light it will be seen to be punctured by a vast number of tiny holes (see fig. 18*a*). It is inside these



18. STRUCTURE OF HYMENIUM IN POLYPORUS BETULINUS.
a. fragment of hymenial layer. *b.* section of a tube.

tubes that the basidia and spores are produced; a single adult fungus may take two or three months to grow, and live for as long again, during which time a great number of spores are produced; a single tree may have a dozen or more of these fungi growing on it. If a log bearing one of these bodies is turned over, while the fungus is still actively growing, it will gradually cover over its spore bearing layer with fresh hyphae and at length form a grey tough layer over it, while the new under surface will become covered by a newly produced layer of tubes; this is usual among all the Basidiomycetes, and is connected with the fact, mentioned in the last chapter, that the basidia can only throw their spores quite a short distance, after which they fall freely; if the tubes containing the basidia opened upwards, the spores could never be disseminated, so that these fungi have had to evolve the habit of always forming their spores on an under-surface, no matter what the difficulties might be.

There are very few of the bracket-fungi which cannot survive the death of their host-tree; *Polyporus betulinus* can live for years afterwards. *Mucidula mucida*, a rather pretty white toadstool which grows on living beech trees, and does

quite a lot of damage to them, appears while the tree is still living, and does not usually survive more than a year after the latter has died. On the other hand *Ganoderma applanatum* which forms thick and very hard brackets of a dark brown colour up to 2 ft across, usually appears before the tree dies, and goes on living (not just the mycelium, but the adult fungus itself) for ten years or so.

A large number of fungi are called "wound parasites" because they can establish themselves on a living host only if it is weakened by disease or injury, and can also attack them when already dead. Those which need only the presence of a slight injury can be serious pests, especially because it is rarely possible to get rid of their spores by preventing them growing in other places; one such is *Stereum purpureum*, which can attack plum trees through pruning wounds, and causes a disease called "silver-leaf", which is very damaging to the crop and eventually kills the tree. Many of this type are too feebly parasitic to cause much harm to human efforts, but we have not yet got enough knowledge of the life history of most of them to be able to assess their true importance. An example of one which has not yet been convicted of serious effect, though it does sometimes appear on living trees such as hazel, is *Polyporus fumosus*.

Of fungi which belong definitely to the second stage, attacking wood *only* when it is dead, the worst are those which can spread rapidly in timber-yards or buildings. Some can destroy the mechanical strength of timber in a few months, while others take longer, and there are some which have little if any effect on the mechanical properties of the wood but by staining it render it unsightly. Most of the latter species, which mainly affect coniferous wood, are Ascomycetes; stained wood generally fetches a lower price in the market, though for many purposes it is not inferior to any other. The suggestion has been made that *Chlorosplenium aeruginosum*, which stains wood a very fine green

colour, might even be exploited for its aesthetic effect, but in fact synthetic stains are cheaper and better. The serious pests among the second-stage fungi are those which cause "dry-rot"; these are all Basidiomycetes, allied to the principal parasitic ones, but belong to several different families.

The chief species concerned is *Gyrophana lachrymans*. This fungus has several interesting peculiarities; one is that after the stage of spore germination is passed, it can live without water, obtaining what it needs by chemical action on the wood, so long as the *air* is not too dry. Another is that it forms thick strands of mycelium, having in them certain hyphae specialized for conducting water, by whose help it can grow over considerable stretches of brickwork or other substance from which it can get no nourishment, and this makes it difficult to control. The *Gyrophana* can establish itself much more easily on wood which has already been attacked by some other fungi, of which *Coniophora puteana* (itself a cause of dry rot in uninhabited and damp buildings) is the commonest; the *Gyrophana* in turn paves the way, by making dry wood moist, for other fungi. Next in importance to this species comes *Poria vaporaria* and other members of the polypore family; these require more moisture in the wood and are thus easier to control. In all cases the most effective means of preventing dry rot is to provide adequate ventilation, which in our climate usually results in evaporating the water produced by the fungus more quickly than it can be replaced. Ventilation alone however is insufficient if the fungus is already well established; general remarks on methods of preventing fungus damage will be made in Chapter XI. Another difficulty with dry rot is that *Gyrophana* is able to produce "chlamydospores", which are segments of the mycelium cut off and furnished with a thick hard wall, able to resist much drought. Thus to arrest an attack by drying out the wood is not always enough to stop it altogether.

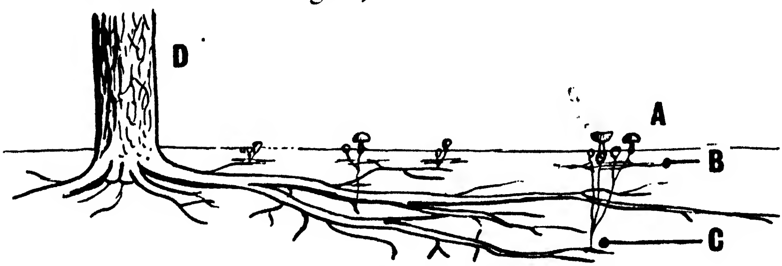
CHAPTER V

UNDERTAKER TURNS GROCER

We have already described fungi as the organisms principally responsible for disposing of the dead bodies of the plant world; and we have seen that it is an easy step from burying the dead to murdering the living. In the conflict thus set up between the plants and the fungi, many new kinds of behaviour have been evolved, which in some cases turn to the mutual advantage of both contending parties. In this and the next chapter we shall discuss the two most important of these beneficial associations.

It seems that during the long ages of evolution, the plants which live year in and year out in the rich soil of the forests, namely the large trees, have been obliged to evolve some means of protection against an increasing number of parasitic fungi attacking their roots. As one would expect, they have not been wholly successful in this, but a number of these assailants have been turned into useful servants of the trees, and (according to one theory) the tables have been in some cases turned, so that the tree has become dependent on the fungus. To take a typical case, let us consider the larch tree: if a young larch be dug up and examined, its roots will be found to bear many short and stunted side-shoots, and even the apparently normal root tips are without the numerous fine root-hairs which grass roots for example always have. If they are examined under the microscope, these swollen rootlets are found to be covered with a weft of fungus hyphae, forming in some cases a dense covering, which, from their universal occurence, would be thought to be a part of the tree, but they belong in fact to a different organism. It is not possible to identify a fungus from the

mycelium alone (mycologists often wish that it was), but by seeing what kind of perfect stage these root-fungi will produce, many have been identified; they usually turn out to be toadstools, and in the case of the larch tree the commonest is the "butter-bolet" (*Suillus elegans*). This is a bright-yellow toadstool with a slimy pileus, having underneath tubes like a sponge instead of the more usual gills; the family of toadstoals which have these tubes is called the Boletacei, and its members are particularly prone to forming mycorrhiza, as this type of association of fungus and tree is called. See fig. 19.



19. THE MYCORRHIZAL RELATION

A general view of the arrangement of the toadstools round an affected tree.

A. the fungi.
B. the ordinary mycelium of the fungi.
C. attachment of mycelium strands to the affected roots.
D. the tree.

Those who have studied the question are very divided in opinion as to the significance of the association for either partner; some have it, as already mentioned, that the tree is, at least in nature, absolutely dependent on the fungus for supplying its requirements of mineral salts, on account of having lost the power of forming root hairs. On the other hand it is a fact that many mycorrhizal trees at any rate can be grown, with due care, without their fungi, and then produce normal root-hairs, and the more commonly accepted opinion is that the tree can usually manage without the fungus, even if in nature it is invariably infected, whereas in many cases the fungus certainly cannot produce its perfect stage in the absence of a suitable tree. Some indeed

claim that it is really a case of parasitism, though the relationship is certainly a less one-sided one than those discussed in the last chapter.

A spectacular instance of the economic importance of mycorrhiza, if not of their biological importance in the strict sense, comes from the investigations of M. C. Rayner in Wareham Forest, Dorset. Here it was found that planted conifers were often a complete failure, and the cause of the trouble was traced to the absence from the soil, which is of an acid nature, of the fungi necessary to form a mycorrhizal association with the trees. Whether it was because the trees could not live without the fungi, or merely that the effort was too much for them, so that they succumbed to the attacks of harmful root fungi which were more prevalent, there can be no doubt in this case of the practical importance of these toadstools in the success of the afforest ation. When the proper fungi were introduced in a suitable compost, then the trees acquired the necessary mycorrhiza, and flourished. There can be little doubt that in many cases at least the persistent association of particular species of fungi and trees, which is sufficiently constant to be a guide in identifying the former, is due to the presence of a mycorrhizal association, even in many cases where this has not yet been proved directly. See fig. 20, which illustrates a proved case.

This delicate balance between two organisms can be easily upset in either direction, so that either the plant or fungus may be killed; there are indeed cases of every grade between a typical mycorrhizon and typical parasitization, but these intermediate grades are best exemplified from a different type of mycorrhiza. In the ones we have described above the fungus grows only on the *outside* of the affected root; but in some cases the fungus actually enters the living tissue, and thus looks more like a true parasite; but it is not necessarily harmful to the plant, and some have it that it is even

20. ILLUSTRATING THE MYCORRHIZAL RELATION
Suillus bovinus growing around the root of a young pine tree; the tree requires the fungus (not necessarily this species,) and the fungus needs the tree.

essential to the life of the plant in some cases. In such a mycorrhizon, the fungus grows only a certain distance into the root, and those hyphae which penetrate too far find themselves digested and destroyed by the plant cells; many of the orchid family are constantly associated with fungi in this way, and cannot ordinarily be grown if their seeds are freed from the fungus (often a very difficult operation, because the fungus hyphae penetrate every part of the plant). However it has been found possible to grow some of these plants without the fungus, by supplying them with various sugars, and thus we have some idea as to the part played by the fungus in these cases. Another example of a

plant, that in nature apparently always contains a fungus which at least does it no harm, is heather; this plant has a plentiful supply of chlorophyll, but it is worthy of notice that many of those which have mycorrhiza of this kind (including many of the orchids) are deficient in green colour, and are therefore not able to supply their requirements of sugars as normal plants do out of the carbon dioxide of the air, and thus live, as do the fungi themselves, at least partly as saprophytes.

The fungi which form orchid mycorrhiza are often members of the "lower fungi", but the constant associate of the orchid *Gastrodia* is the honey fungus (*Armillariella mellea*), which is interesting because this fungus is a serious pest of many trees, especially in the tropics (though it attacks apple trees in this country as well), being a root parasite. It has long "rhizomorphs", that is to say strands of mycelium with a hard blackened outer bark, which grow considerable distances in the soil from one tree to another. Sometimes they succeed in establishing themselves in the living tissues of the root, and in time kill the tree, but it seems that the *Gastrodia* has found means of preventing its attack and indeed of turning the fungus to useful account.

Despite their admittedly considerable importance in forestry, however, mycorrhiza-forming fungi are of less consequence to mankind than they might be, because most of our food crops are undoubtedly independent of this type of association; indeed the smaller grass-like plants of our pastures, and the large grasses grown for grain, because of their shorter life, have been less exposed to the possibility of being killed by root parasites than the large and long-lived trees, and thus we may suppose have not been obliged to evolve this elaborate means of defence against such parasites. This is not to say of course that there are no fungi which attack cereals by their roots; there are many, and some are very serious pests.

CHAPTER VI

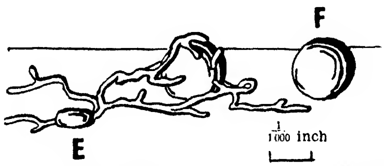
PIONEERS

THE formation of mycorrhiza is not the only way in which fungi have been able to be of service to plants or to the general economy of nature; there is another type of co-operative enterprise which certain fungi have undertaken, which may be even more significant, for life as a whole, than the one we have described; this is exhibited by the lichens.

A lichen is a fungus which has overcome its inability to make its own food, as plants do, by using the energy of sunlight, by borrowing the chlorophyll mechanism of certain primitive plants. We ought not, of course, attribute purposiveness either to evolution or to the development of a single organism, and the life history of lichens is a good example of this; for despite their admitted success in propagating themselves each one is to some degree the product of chance, as we shall see. However, whatever their origin, lichens can best be regarded as fungi which can live like plants, and it is as such that we shall describe them. There is no doubt, for example, that the dominant partner in the lichen association is the fungus; it is the fungus which determines the shape of the lichen (the plants are mostly single-celled types having no powers of body-building), and it also controls the growth and reproduction. Only the greenish colour which most lichens have is due to the presence of the minute plants, and even this is often obscured by other pigments made by the fungus, yellow, red, and black being common colours.

Let us describe the life history of a typical lichen. The scene of action is a dampish face of bare rock on some mountain-side; the only vegetation there consists of a few

one-celled plants called algae, blown there from some more favourable spot, such as a pool of water which has dried up; they are almost certain to perish, for such plants cannot live for long without water. However, just in time, a gust of wind carries a fungus spore onto the rock face, very near to where these algae are; not only that, but it happens to be a spore of one of the particular fungus species which could be of use to the algae at that moment. The chances against this are extremely great, but it does sometimes happen. The spore germinates and, attracted in its growth by a chemical effluvium of the algal cells, its hypha grows towards them; it branches rapidly, and begins to envelop them, as illustrated in fig. 21. Before long the fungus has made a little parcel of algae a few thousandths of an inch across. By that time, perhaps, the rock face has dried, and most of the algae which happened to be about will have died, or passed into a state of suspended life as many of these primitive plants can if circumstances become unfavourable; but the lucky ones, protected by the fungus, will continue to thrive. They have to pay for this by giving up a part of their accumulated sugars, and probably other substances, to the fungus. Just what the relationship between the two organisms is we cannot say, because lichens do us no harm, nor are they cultivated, so that money has not been available for enough research to be done on it. Despite the tax which the fungus levies on the algae, they continue to grow and divide, though at a diminished rate, and the increase of the algae continues to keep pace with the growth of the fungus. Unlike most fungi, lichens grow very slowly, probably because they are limited by the growth of the algae, which cannot be very



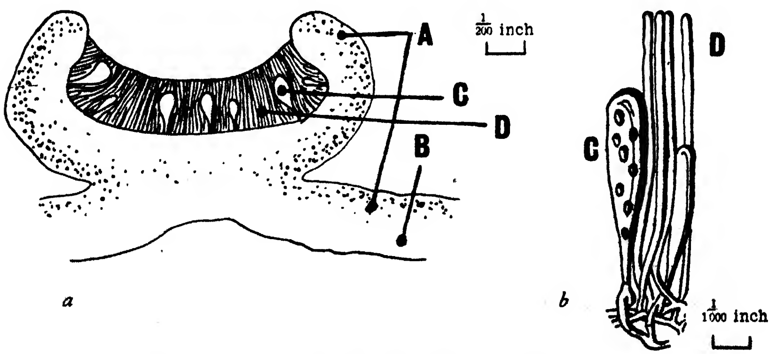
21. GERMINATION OF A LICHEN SPORE NEAR SUITABLE ALGAE
E. germinating spore.
F. algal cells.

fast because most of their surplus is diverted for the benefit of their protector.

Lichens may be up to a tenth of an inch thick, but they keep the algae within a very short distance of the illuminated surface, so as best to enable them to perform their food-producing functions. If the lichen is of the kind which grows like a crust over the surface of rocks or bark of trees, it may be peeled off, and the underside seen to be white in colour, due to the absence of algae on that side. Many lichens form branched or leaf-like structures, which help to admit the maximum sunlight to the imprisoned plants, and it is possible that some of the bright colours produced by certain kinds have an effect on the sugar-forming powers of the algae, since in the free state it is known that the colour of the light reaching green plants has an important effect on its usefulness to plants.

Sooner or later, our embryo lichen will reach that size (it does not have to be very big) at which it will begin to give off from its surface little fragments, from a two-hundredth to a twentieth of an inch in diameter containing fungus hyphae together with a few wrapped-up algae. These bodies are readily blown about, and serve as the chief means of dispersal of the lichens; with some, very probably, they are almost the sole means of reproduction, because of the improbability of the required combination of fungus and alga coming together by accident. Nevertheless all lichens do produce their own fungus spores, which only under these rather exceptional conditions can serve their purpose; we will explain below why it is that they continue to find them necessary. These spores are produced in special organs, which (among fungi of the Ascomycetes) are called ascocarps. These are formed on the exposed surface of the lichen when conditions are favourable (we don't know yet what conditions are "favourable"), and often take the form of small disc- or saucer-shaped bodies, which may reach a dia-

meter of $\frac{1}{4}''$. Sometimes they have a distinct border, which may or may not contain algal cells, and sometimes no border. Fig. 22 shows a typical lichen ascocarp in cross section: the algal cells are represented by dots at A, the purely fungal part of the body being indicated at B. The spores themselves are produced in a special type of cell, called an ascus, shown in fig. 22*a* and *b*, C; this type of spore-bearing cell is characteristic of the great group of fungi called Ascomycetes, just as the basidium (fig. 4, p. 22) is of the Basidiomycetes; in addition to the lichens the Ascomycetes comprise a great number of species of fungi, which taken as whole are of much more economic importance than the Basidiomycetes. In the lichen ascocarp (which is not essentially different from those of other Ascomycetes) these asci are packed in among a number of much thinner, and usually longer cells, called paraphyses (fig. 22 *a* and *b*, D). The ascus, when it is mature, forms eight spores (occasionally less, rarely more) which appear floating freely in the interior of the cell (a very unusual way to form any kind of cells, by the way), and when ripe the ascus bursts. Its wall is elastic, and the liquid inside is under considerable pressure, so that the contained spores are shot away for some distance.



22. SPORE-BEARING ORGANS OF A LICHEN

a. diagrammatic section of an apothecium. *b.* part of the hymenium.

A. tissue containing algae. C. ascus.
B. tissue without algae. D. paraphyses.

Unlike the basidium, the ascus is thus in itself quite an effective agent of spore dispersal, and can throw its contents up to half an inch into the air; thus the Ascomycetes find no need of the elaborate apparatus to ensure that their spores are produced on a downward-facing surface, such as we have pointed out is common to almost all Basidiomycetes; on the whole Ascomycete fungi are less complicated in structure than Basidiomycetes, and often their spore-bearing surfaces face upwards, as they do in most lichens.

The ascus resembles the basidium in that when it is first formed it contains two nuclei, which later fuse together, just before the joint nucleus divides to form the spores; the Ascomycetes do not, however, have the elegant process of diploidization, described in Chapter III, like the Basidiomycetes, but only a few of the hyphae in the ascocarp have paired nuclei, the rest being uninucleate. It is because the formation of ascospores, like that of basidiospores, involves the mixing and re-dealing of the hereditary characters of the species, and thereby speeds up the process of variation and evolution, that this mode of reproduction is necessary to the lichens, despite its small apparent chance of success.

The most important thing about the lichens from the point of view of world economy, is that their habit of "using" the energy of sunlight by the help of their algae enables them to combine the independence of a plant with the chemical versatility of the fungi. This chemical versatility is in a sense nature's compensation to them for having lost the power to manufacture their own food, without having the ability to seek actively for special food as the animals do; for without it they would have had little chance to make good their claim to the variety of decomposed and cast-off organic compounds on which they have to subsist. In the case of lichens this unique combination of powers makes them the best colonizers of uninhabited territory which other organisms are unable to invade. They can not

only derive their food from the air, but can contrive to dissolve even the most refractory materials, such as many of the silicate rocks, which defy the action of most of the chemist's reagents. It is true that there are rocks which even the lichens cannot touch, but they are not common. After the lichens have been growing for some time on such a rock face, the disintegrated rock, and a certain amount of organic debris from the lichen itself (this accumulates very slowly), forms a tiny patch of "soil", in which the hardiest of plants can get a foothold; usually the first to appear are mosses. Eventually these plants provide enough organic matter to support a more varied flora, and at length, by gradual stages, the bare rock may be rendered fertile enough to support forest trees. This process is far too slow to be of much practical interest to the farmer, whose great-grand-children would not live to see it completed, but there can be no doubt that it is of considerable importance in the general history of life on the Earth, and there must be many places where before lichens had been evolved (it is a pity that we can form as yet no estimate of when this was) there could have been no life, but which, as things are, are fertile and luxuriant.

All lichens in the strict sense are Ascomycetes, but it is believed that the lichen-habit, strange though it seems, has been evolved several times by different families of Ascomycetes, and in classification it is necessary to scatter the lichen families about among several different groups of fungi. It is all the more odd that what has evidently proved so attractive a mode of life to one sort of fungi, should fail to enlist any recruits from the sister-group of the Basidiomycetes, to which the toadstools belong, though the two are about equally progressive in most respects. There are one or two species of bracket fungi which commonly have algae growing in their tissues, and these have been called basidiolichenes, but it is a misnomer, for there is no true organic

relation between the organisms, and the fungus can exist quite well without the algae. There is a family of Ascomycetes which, from the curious shapes they grow in, are believed to be lichens which have reacquired the power to do without their green partners.

Lichens have been used sporadically as food by various nations, and it is traditionally supposed that the manna of the Israelites was a species of lichen; but they probably never form an essential article of diet except in times of famine. The name reindeer moss is applied to any bushy kind of lichen growing on the ground, and it is a fact that reindeer and other herbivorous animals in Northern countries do subsist to some considerable extent on lichens, so that in this way they are of indirect service to man. Many peoples, including the tweed-makers of the Scottish Highlands, use lichens as a source of natural dyes, and some are so employed commercially; litmus is perhaps the best known product of this class. Recently certain acid substances found in lichens have been observed to have an action on bacteria, and may be of use one day in medicine, but if so will almost certainly be better to make the materials synthetically than to rely on such small and slow-growing organisms to provide them.

CHAPTER VII

A FAMOUS FAMINE

So far we have been mainly describing objects which are quite familiar to most people; maybe mycorrhiza are not very well-known, but the toadstools which are their commonest cause are conspicuous objects in our woods, and conspicuous too, to anyone who can recognise a few species, is the habitual association between particular fungi and particular trees. Now, however, we have to consider a kind of fungi which usually cannot be seen except under a microscope, but for economic reasons, as will presently appear, we know more about these fungi than about the more familiar kinds.

A hundred years ago people would have laughed at the idea that these minute fungi, which the microscope had revealed, could be of any importance to mankind. But ideas changed when the English clergyman Berkerley proved that one of these had been the effective agent in the terrible famine that ravaged Ireland in 1845-6. The introduction of the potato into Europe had done an immense service to its inhabitants, in affording them a staple food which could be worked into the rotation of crops, such as it was, so as to replace the unproductive fallow or the relatively unnutritious turnip by a crop which gave as much food as the cereals. Especially was this so in Ireland, where the climate was more favourable to growing potatoes than corn, and where the standards of life were depressed owing to the colonial status of the country.

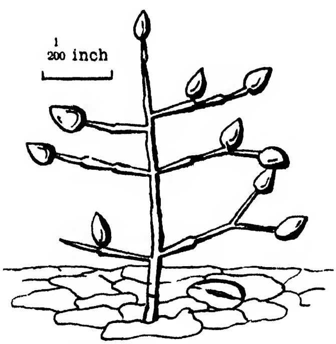
But every crop has its pests, and the fungus, which we now know as the causative agent of the destructive "blight"

of potatoes, must have existed among them for some time, though in a non-epidemic form. What were the immediate causes, which led to the Irish disaster in 1845, we may never exactly know; it was not the first record of the disease, but so little was then known about the nature and cause of plant diseases that we cannot deduce much from the casual reports which we have from various Eurpean countries. The most probable conjecture is that the fungus had lived in the Andes on the wild and cultivated potatoes (the wild types have often a much greater resistance to this and other diseases than their cultivated descendants), but had never done much damage; there is, for example, no record of serious potato failures in the empire of the Incas, whose subjects would certainly have taken note of anything approaching the Irish outbreak. But on their introduction into Europe, the potatoes were selected for increased yield, without any suspicion of the existence of the disease, until at length some spores got corried over the Atlantic by chance, and at the first occurrence of favourable weather conditions, started an epidemic. Within seven days so great a part of the potato crop was destroyed, that, as a result of actual deaths from famine and still more from subsequent emigration, the population of Ireland was reduced to less than half what it had been, and has never since recovered.

Actually the famine, though not the blight, was preventible, in that corn was available in sufficient quantities to have averted it; but owing to the inaction of the government it was not requisitioned and distributed in time. The famine had however more positive political consequences, for it not only excerbated the Irish against the British, but played an important part in hastening the repeal of the corn laws. It also promoted scientific interest in plant diseases in general, and may fairly be said to have brought about the beginnings of plant pathology, as this science is called. All the same, a long time passed before men of science were convinced that

fungi were the main agents of plant disease, as we now know them to be.

The life history of the potato blight fungus, which is called *Phytophthora infestans*, may be described as follows. The spore germinates on a leaf of a potato, or on the tuber, and puts forth a narrow germ-tube in much the same way as the spores of toadstools do. This germ-tube enters the tissues of the potato, which it kills, and branching rapidly gives rise to the mycelium of the fungus; this mycelium differs from that of the Basidiomycetes and Ascomycetes, however, because the hyphae do not have cross walls, except in the special branches on which the spores are borne. These, of which one is illustrated in fig. 23, grow out from the surface of the leaves, or of rotten tubers; they are called sporangiophores. The reproductive bodies, properly called zoosporangia, which they bear are not the same sort of thing as the imperfect spores or conidia of Ascomycetes. They may, if there is not much water about, as on the surface of a potato leaf as described above, germinate by means of a germ-tube; but there is another thing they can do, namely to give out their contents in the form of a number of very small bodies, having each two fine hairs attached, by means of which they swim through the water. Because they resemble little animals they are called zoo-spores; they are very frequent among the Oomycetes, to which group the blight fungus belongs, but the sporangia can usually behave as spores under dry conditions, and some species have lost the power to produce zoospores at all. In some Oomycetes,



23. SPORANGIOPHORE OF PHYTOPHTHORA INFESTANS growing on a leaf.

but not *Phytophthora*, the sporangia first give out zoospores with swimming-hairs at the front end, which swim about for a time and then settle down and draw in their swimming hairs. But instead of germinating to produce a mycelium they presently extrude their contents in the form of another zoospore, this time having a different shape, with swimming-hairs at one side; after a further period of swimming this one does grow out into a mycelium. It is rather difficult to see that this performance can be of any advantage to the fungi concerned.

Most Oomycetes have another kind of spore which they can produce, besides sporangia, called oo-spores; these are fairly large, over a thousandth of an inch across, and have hard crusts. They are formed singly in the tissues of the diseased plant. Their function is in one respect similar to that of the asci and basidia of higher fungi, because they are formed by the coming together of two hyphae, and in them fusion of nuclei takes place; but in this case it is possible to distinguish "male" and "female" organs. Thus the oo-spores serve for sexual reproduction. They are resting bodies, enabling the fungus to live through unfavourable periods, rather than agents of dispersal, because they can germinate after a very long time (even many years). They do so usually by producing a sporangiophore, but those of the potato blight have never been seen to germinate at all.

The main incentive to elucidating the life history of a fungus which is a pest of crops is to find out how best to kill it and prevent the damage it does; we shall not in this chapter say much about the methods of doing this in general, which we shall reserve till Chapter X; but despite the fact that it was the first plant disease at all clearly understood, it was not the occasion of the first successful efforts to apply preventive measures. Indeed it was long before effective measures came to be used against the blight, either in Ireland or elsewhere. In those days the vine was reckoned as a more

important crop than the staple food of an unimportant colonial people, and thus fungicides were used in viticulture before potato-growing. Nowadays it is the regular practice, among all farmers who can afford it, to spray potatoes several times in a season with Bordeaux mixture (a mixture of lime and copper-sulphate), or some similar fungicide. Recently in some countries, first in Holland, there have been issued to farmers regular predictions of the times when a blight epidemic is most likely to start, this being usually in warm muggy weather of a kind fairly easy for meteorologists to forecast; by taking note of these predictions, a considerable saving of fungicide can be made and the cost of production thus reduced. Many other diseases of crops are tied up with the weather, but as yet neither plant pathology nor meteorology are sufficiently advanced for much use to be made of what knowledge we have.

CHAPTER VIII

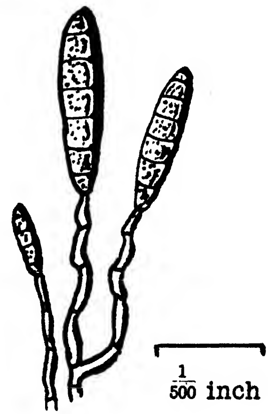
ROBBERY

NATURALLY, in so numerous and versatile a group of organisms, there are countless variations on the theme of fungus parasitism. These have arisen in various ways out of the perpetual conflict between the plants, which managed to survive only if they were equipped with adequate means of defence against the attacks of invading fungi, and the parasites themselves, which likewise perished if they did not inherit the power to overcome the defences of their hosts.

Probably the earliest parasites simply made no distinction between a living host plant and its dead remains; but there are not now any plants so inept at countering fungal attacks as not to put up some kind of resistance. The commonest means of defence is to form what is called a "necrotic area" around the point of entry of the fungus; that is to say, a patch of dead cells, in which the fungus cannot grow and through which its hyphae cannot easily penetrate. A slightly better and also very common response is to surround the necrotic area with a layer of cork; this is in fact the normal answer of most plants to any mechanical injury to their living tissues, and serves them in the same stead as the clotting of our blood serves us, in preventing the sap flowing out and the wounded tissues from drying up. Those fungi which have not evolved the chemical agents necessary to prevent the cork cells being formed, or to grow through them if they are, usually reveal their presence as discoloured spots on the leaves or stems of the plants affected. If the plant is an annual, or a deciduous tree, these spots are not usually very serious to it, but they may be important to the farmer, who is interested in producing the maximum yield of food from the minimum area, and therefore cannot avoid

providing the fungus with conditions far more favourable to its spread than it ever finds in wild nature; and example of this is provided by a microscopic Ascomycete called *Pyrenophora* (fig.24) which causes a leaf-spotting of wheat, which, though it never actually kills the plants, can cause quite a serious reduction in the yield of grain. Usually however leaf spots are less troublesome than the diseases caused by fungi able to avoid the localising responses of their hosts; these affect the whole plant, or the greater part of it, and are called "systemic" diseases.

Potato blight, described in the preceding chapter, is a typical example of this type; another is the tomato wilt illustrated in fig. 25. These usually kill their victims in quite a short time, as potato blight does, and in so doing set a period to their own survival. This problem of how to carry on in the season when the host plant is not available occurs to all parasitic fungi. The blight fungus survives the winter in the perennial tubers of the potato which are too large for the fungus to destroy rapidly; but this method will not serve for the parasites of annual plants which pass the winter as seeds, nor is it adequate for parasites so virulent that they destroy their host within a season. Of course many fungi which follow this mode of life are not obligate parasites, that is to say they can also live wholly on dead organic matter, though often they cannot complete their life cycle in this condition; for these there is no problem. An example is afforded by



24. SPORES OF PYRENOPHORA GRAMINEA

These are the conidia or "imperfect" spore form, which are produced without fusion of nuclei, and independently of the asci.

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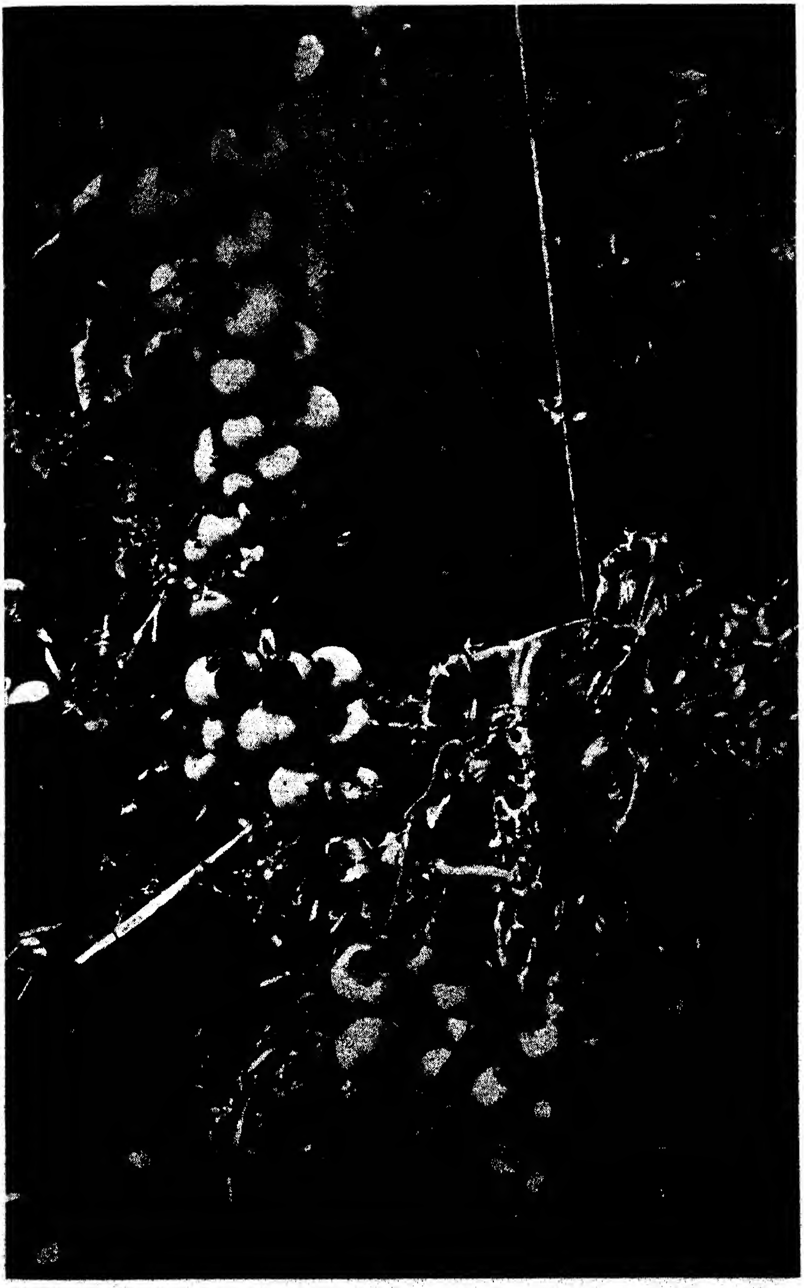
25. A SERIOUS PLANT DISEASE

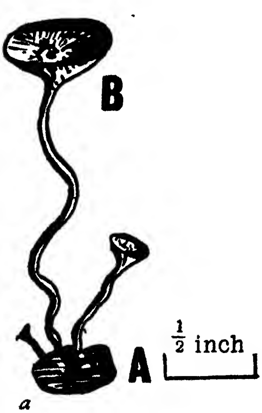
Tomato wilt.

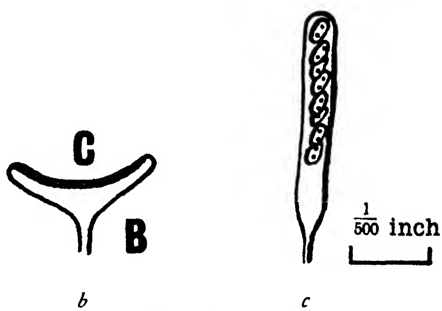
A healthy and wilted plant growing side by side.



Ophiobolus graminis, the cause of the serious "take-all" disease of wheat. This fungus can live for many months in the soil, but must adopt a parasitic existence if it is to complete its life cycle by producing its spores.

Many fungi get over the lean period by means of special organs of their own. *Sclerotinia fructigena* lives during the summer as a parasite of the leaves and young fruits of the apple, causing a brown rot which is often very widespread. When the apples fall it forms a hard compact mass of hyphae inside, called a sclerotium. If it gets buried, this puts forth in the spring ascocarps (shown in fig. 26) which are built on the same general plant as those of lichens, but are much bigger, up to an inch across, and furnished with long stalks which enable them to rise above the ground level (see fig. 26). The asci formed in these bodies liberate the ascospores, which reinfect the young leaves of the apple trees.





26. SCLEROTINIA FRUCTIGENA

a. sclerotium A producing ascocarps B.
b. section of an ascocarp, showing position of hymenium C.
c. an ascus, with eight spores.

Relatively few species have overwintering bodies so large as those of *Sclerotinia*, whose sclerotium may be over half an inch across and the stalk of the ascocarp up to six inches). Usually, as in the case of the mildews described in chapter IX, these resistant bodies are microscopic, and many fungi, like the annual plants themselves, pass the unfavourable

season in the form of special resting spores; these are single cells furnished with a thick wall able to keep the spore from drying out, and are unable to germinate until they have been maturing for several months. Some have evolved the power of following their hosts into their winter fastness even to the seed itself, and some of the most troublesome crop diseases are caused by fungi which get into the plant when the seed is being ripened, and appear when the latter germinates. *Ustilago nuda*, the loose smut of barley, grows inside the plant without giving any sign of its presence until the ears are produced and then, instead of pollen being formed, the anthers contain the black spores of the fungus, which get carried by the wind just like real pollen grains, and if one alights on the stigma of a barley flower it sends down a germ-tube of the fungus alongside the pollen tube, and so infects the developing seed and produces an infected plant when the seed germinates.

All these devices are fairly obvious; but they are not the only characteristics which a successful parasite has to evolve in order to survive; we have already mentioned that many plants can produce cork around a young fungus mycelium attempting to gain a foothold on it, but without doubt a more important defence with most plants is a chemical one, and the fungus, in order to meet it, must have a chemical reply. We are as yet too ignorant of the subject to be able to say what this defence is, but in some cases probably the plant can make substances able to coagulate the protoplasm of the fungus, (the socalled "antibody" reaction) just as our bodies are able to do against various disease-causing bacteria; but whereas animals, when they recover from a disease in this way, often acquire a fairly lasting immunity from future attacks, plants rarely if ever do so, perhaps because they are continually growing new tissues. It is a very difficult problem for a fungus to overcome this type of defence; bacteria attacking us are quickly carried to every part of the body

in the blood, and multiply as they go, but a plant is usually only attacked by quite a small number of fungus spores; with us, a disease may take hold before our defences get into action, but a plant can often isolate an incipient attack before it has spread very far.

Two courses appear to have been found possible to fungi to get over this; some have evolved a chemical immunity to the hosts defences (it sounds easy, but in fact only a few groups have been successful in this line) while others have adopted the more violent course of destroying the cells of the host rapidly enough to evade any possibility of their chemical retaliation. The second method has the disadvantage for the fungus that if the attack is successful the whole plant will fairly soon succumb, leaving the fungus to find a fresh victim, and necessitating some effective adaptation to survive these frequent crises, such as we have already remarked on the problem of overwintering. Most of the fungi which use these methods belong to relatively primitive groups, such as *Phytophthora;* the difficulties of the death of the host are less acute in the case of large trees and we accordingly find that many of these relatively undiscriminating parasites which attack trees belong to higher groups, such as the Polyporacei, which have not found it necessary to evolve any other mode of attack. Furthermore, most of them are only semi-obligate parasites, and can and do survive the death of their hosts, as we saw in Chapter III for *Polyporus* and in Chapter VII for *Phytophthora*, which can continue to live in rotten potatoes for some time.

The drawback of the first method of combatting the chemical resistance of the host, by evolving a specific chemical immunity, is that having once achieved the necessary adjustment to the possible defences of the living cell of the host, the fungus is incapacitated from attacking any other species of plant; for, as we now realize, every species of organism is distinguished by a particular set of chemicals out

of which it is made, so that there is a distinct difference in the environment which a fungus will meet inside the cells of any plant at all other than its normal host, and even between races in one species. Thus the chance of a spore of such an exacting parasite finding itself on a plant on which it can successfully establish itself is much smaller than that before a spore of one of the "Blitzkrieg" type. Of course the same principle applies, in less degree, to all fungi; and while those which quickly kill their host cells have nearly always a wider range of victims than the more skilful parasites, it is very few fungi that can live on a really wide variety of plants as true parasites; perhaps one of the least exacting in this respect is *Pythium deBaryanum*, an Oomycete, which kills the seedlings of a great variety of cultivated (and wild) plants, and, significantly, it is exceptionally virulent, and kills its little victims sometimes in a few days, and can also live saprophytically in the soil.

On the other hand, of all fungus parasites those which have gone farthest in the direction of not injuring their hosts are also those which are the most restricted in their choice of victims, namely the rusts and mildews which we shall describe in the next chapter.

CHAPTER IX

THE VIRTUOSI

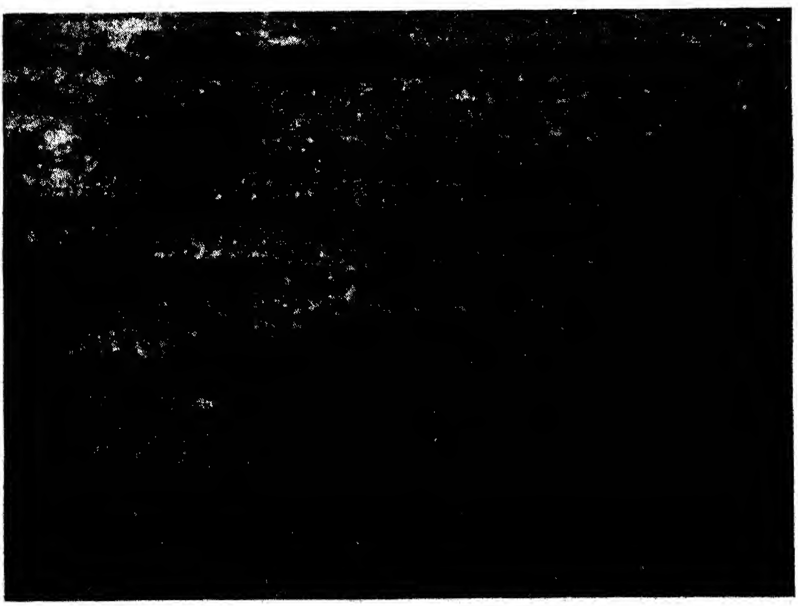
I have mentioned that certain families of fungi have evolved such proficiency in the art of parasitism that they may be called the "virtuosi" of this mode of life; the chief of these are the rusts and mildews, which will be described in more detail in this chapter.

Not only are rusts important to study because of the damage they do to our crops, which in some countries is extremely serious, but as examples of nicely balanced organization and complexity of adaptation to a particular mode of life they are hard to excel. Rusts are reckoned as a subclass in the phylum of the Basidiomycetes (which include also the toadstools, puffballs, etc.), and though they do not look very like the more familiar fungi (see fig. 27 and fig. 28), they agree with them in producing their spores on basidia which are similar in general plan, though different in detail, from those of the toadstools. However, their life history is much more complicated than that of the fungi we have discussed up to now, and to illustrate it I shall describe the black rust of wheat, common in Britain and very serious in America, known as *Puccinia graminis tritici.*

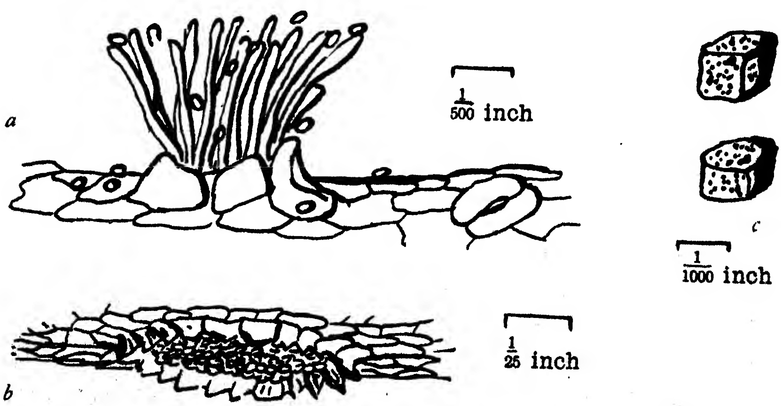
Let us begin the story from the basidiospore. If one of these spores is lucky enough it may land on the leaf of a barberry bush; in that case it will germinate, and presently the germ-tube which it puts out will penetrate the cuticle of the leaf. The cuticle is fairly thick and hard, and it is remarkable how the little hypha manages to penetrate it; the hypha, like most living cells, has a wall through which water can pass, but substances dissolved in it cannot get through; a vessel with such a wall tends to suck water

27. RUST ON A ROSE SHOOT
The caeoma (primitive type of aecidium) of *Phragmidium disciflorum*, shown at A.

28. UREDO-SORI of *Puccinia glumarum tritici* on a wheat leaf.



from outside into itself, thereby generating a pressure inside which can be considerable; in the case of fungus hyphae it may be about 200 lbs per square inch. This however is not nearly enough for the purpose in hand, for which something like 5,000 lbs per square inch may be needed; the necessary step-up is obtained by the hypha forming a very small weak spot in its wall on the side in contact with the leaf, upon which the whole of the force derived from the rest of the cell is concentrated; by such means some fungi have been shown able to penetrate thin sheets of metal foil. Once within the tissues of the barberry leaf, the hypha branches profusely and soon forms an extensive mycelium. This mycelium proceeds to form two kinds of reproductive bodies; the first of these are called spermogonia, and are minute pustules appearing on the upper side of the leaf, consisting mainly of specialized hyphae from whose tips very minute spores called spermatia are cut off; one is illustrated in fig. 29*a*.



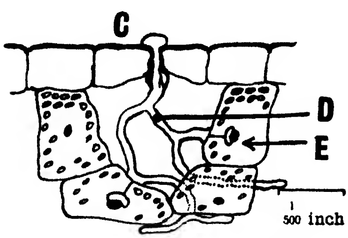
29. RUST ON ITS SPRING HOST

a. spermogonium, general view. *b*. aecidium, general view. *c*. accidiospores.

The spermogonium secretes also, probably by means of other special hyphae, a sweet tasting liquid, and makes the plant produce red pigment in a little spot around it. Thus the fungus, by the bright colour and sweet "nectar", attracts insects, by whose movements the spermatia are detached and carried away, just as pollen is in the case of flowering plants. The object of all this is to facilitate the bringing together of the two (or possibly more) "sexes" of the rust, for as in the case of the toadstools the basidiospore produces a mycelium having cells with one nucleus in each, whereas for complete development a bi-nucleate mycelium is required, and only certain combinations of "sexes" are fertile together. If two suitable mycelia are established together on the same leaf, they may diploidize one another without the aid of spermatia, but more often this does not happen, and complete development must wait on the arrival of an insect from another leaf seeking for spermogonial nectar, and carrying a few spermatia of the right kind. The latter stick to one of the special receptive hyphae in the other spermogonium, and at once the nucleus in the spermatium (it contains little material outside the nucleus) passes into the receptive hypha and begins repeatedly to divide, and at length provides a partner to every nucleus in the mycelium. The spermatia thus function not unlike the pollen of plants or the spermatozoa of animals, but differ from either in that both "sexes" produce both them and the receptive organs which they fertilize.

Once diploidized, the mycelium begins a new phase of activity; it produces a new kind of organ called an aecidium, in which aecidiospores are produced. The aecidium is like a little cup, as shown in fig. 29*b*, which opens on the under side of the leaf, and contains a large number of largish, rather square-shaped spores full of yellow oil-drops, which give the whole a bright yellow colour; the spores may reach 1/1000 of an inch across. These, like the my-

celium which has produced them, contain each two nuclei. They cannot germinate on a barberry leaf, however; instead they have to alight on the leaf of a wheat plant before they can continue their life history. Furthermore they are very particular as to what variety of wheat they find; on some kinds they get no farther than to reach a stoma or breathing-pore of the leaf, and cannot enter it; on others they can enter, but soon die; on others they can produce a feeble growth, and only on a few special kinds can they flourish. But all this does not help the farmer, for there are spores able to attack most varieties of wheat, even if a particular spore is very restricted in its powers; it is a very interesting problem to work out how the different "races", as they are called, are inherited, for it is known that all races can interbreed, via their spermatia on the barberry, and that new races from time to time appear, so that the task of breeding varieties of wheat resistant to all known races of the rust is apt to be a disappointing one.



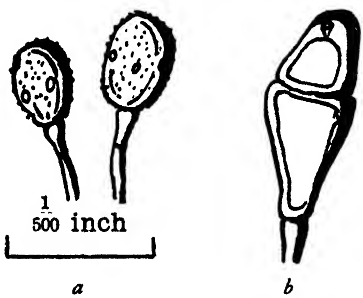
30. RUST HYPHAE INVADING A WHEAT LEAF

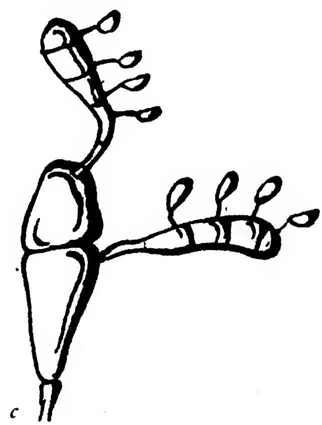
C. penetration vesicle over a stoma.
D. hyphae growing through the air spaces in the leaf.
E. haustoria, on very thin stalks, pressed against the nuclei of the cells.

If an aecidiospore manages to establish itself in a wheat leaf, it produces a mycelium having two nuclei per cell, which branches between the cells of the wheat, and only draws nourishment from them by means of special very narrow side branches which swell out into tiny sausage shaped bodies at their tips, usually touching the nucleus of the wheat cell (fig. 30). By means of these haustoria (as they are called) the fungus contrives to draw a living out of the wheat with the minimum of damage to its host; for a cell containing a haustorium of the rust is in some cases

at least bigger and better than an uninfected cell. It might be asked, if this is so, why need the farmer worry? The answer is that the farmer makes demands on the wheat far greater than nature does, and that under the conditions of unnatural overcrowding with a single species such as prevail in a wheat field the rust is apt to increase beyond the point at which the plant can spare it surplus food; the unnaturally high yield of grain from the cultivated plant is cut down to an extent which would not stop its reproducing itself in nature but may well stop the farmer from getting a profit on his labour.

The binucleate mycelium in the wheat produces two kinds of spores (figs 31, *a*-*b*): during the growing season it gives off a vast number of "uredospores", which serve to establish new mycelia on previously uninfected wheat leaves, and thus make up, by their numbers, for the relative fewness of the aecidiospores, whose production comes to an end early in the year. At harvest time however the rust goes





31. RUST SPORES
FORMED ON ITS SUMMER HOST

a. urdospore.
b. teleutospore.
c. germination of teleutospore, forming basidia.

over to producing a new kind of spore, called a teleutospore, as in fig. 31*b*. Whereas the uredospores are brown the teleutospore is nearly black, and moreover it always consists of two cells stuck together. Unlike the uredospore, the

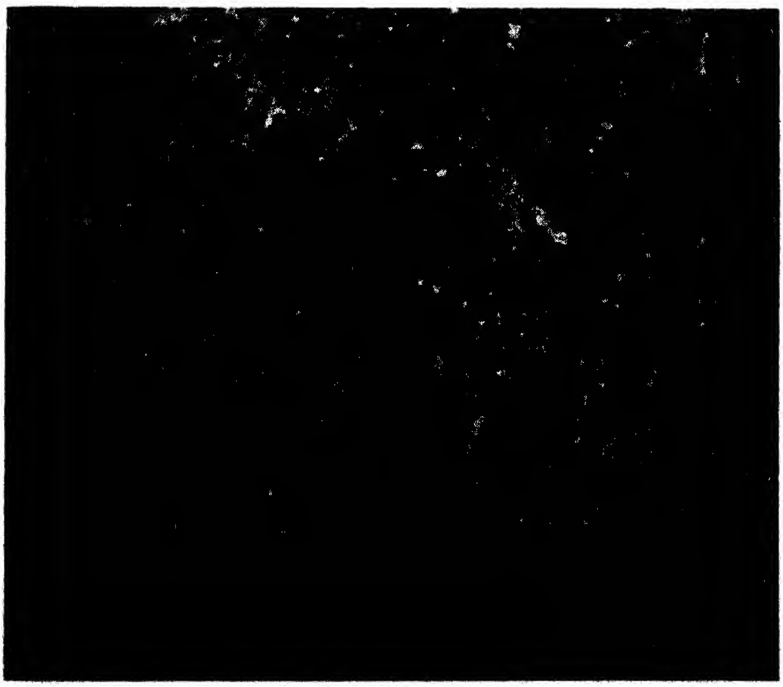
teleutospore cannot produce a mycelium; in fact it can't do anything for several months, but when it has been exposed to low temperatures for a sufficient time it is able to germinate, and does so to form a single basidium from each cell. We saw how in the toadstools the two nuclei which are found in the young basidium join together in it before dividing to form the four basidiospores. The same happens with the rusts, except that it is in the teleutospore that the fusion takes place; the basidia themselves are divided by crosswalls into four cells, each of which bears one spore on the end of a long slender stalk, corresponding to the stalks at the tip of a mushroom's basidium, and like them throwing off the spore by a tiny explosion. The basidiospores then reinfect the barberry bushes, and so round the year again.

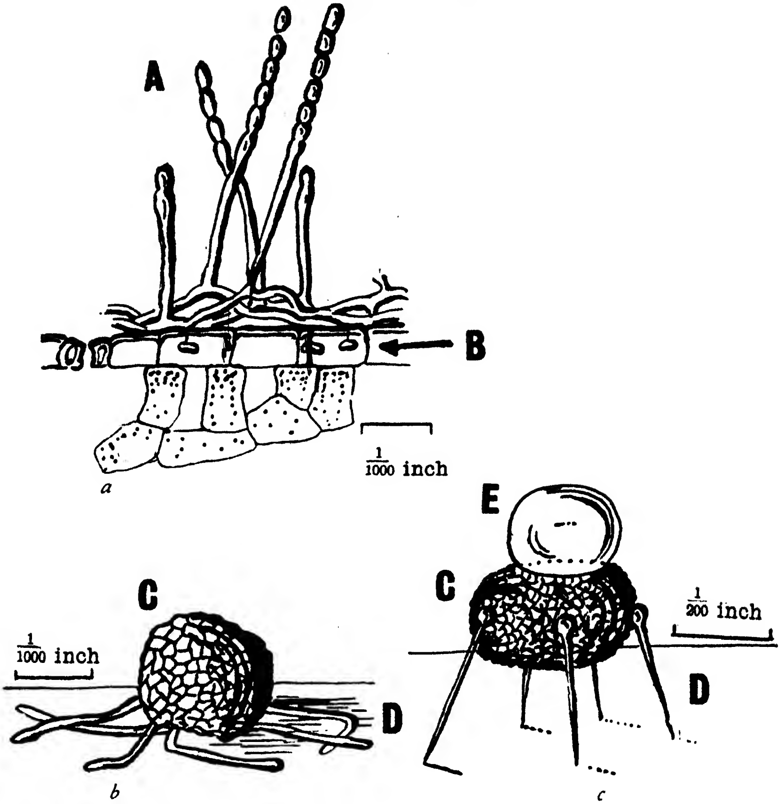
Not all kinds of rusts have so complicated a life history as this, involving two hosts, but many of the economically important ones do have, and one is tempted to ask what the fungus gains by this behaviour. It is hard to answer this, but it may have some connection with the fact, that natural selection acts much more rigorously on organisms having only one set of hereditary factors, such as the uninucleate mycelium of the rusts, than on those having a double set, in which an unfavourable character may be masked by the effect of the corresponding gene in the other set. Thus a uninucleate fungus gets less chance to evolve the very elaborate adaptations required, if it is to do so little damage to its host as the rusts do, than a binucleate one. Since fungi have to spend at least part of their life in the uninucleate state, it may be that the degree of perfection shown by the rusts in their parasitism could only be acquired by the device of separating the uninucleate and binucleate stages on separate hosts, so that the selection of the characters giving the fungus power to live on its summer host should not be spoilt by the occurrence of the uninucleate stage, which is necessarily less adaptable, on the same host.

The other group of fungi, whose parasitism can be called as "careful" as that of the rusts, is the mildews, known scientifically as the Erysiphacei; one is illustrated in fig. 32. These fungi form their spores in asci, like lichens but unlike rusts and toadstools; they are quite unlike rusts in their structure and way of life, but like them they do remarkably little damage (biologically, not agriculturally) to their hosts; because of that they are very restricted in their host range, though they make up for this, again like the rusts, by having a diversity of races able to attack different varieties of plant of the right species.

The ascospore of a mildew, if it alights on the right kind of leaf (or fruit) germinates and puts out a germ tube which

32. MILDEW
Erysiphe graminis on a wheat leaf.





33. MILDEW

a. diagrammatic section through leaf on which the mildew is growing.
b. ascocarp or "perithecium" of *Erysiphe graminis.*
c. ascocarp or "perithecium" of *Phyllactinia corylea.*

A. conidiophores with chains of oidia.
B. epidermis of host, with haustoria.
C. body of perithecium.
D. appendages, which (in b) serve to attach it to the host, but in (c) are hinged and moveable, and raise it up in dry weather.
E. drop of sticky secretion, by which the raised up perithecium adheres to a passing animal.

does not ever make extended growth inside the tissues of the leaf (this does not apply to some of the more primitive mildews), but, by a mechanism apparently exactly similar to that used by rusts, penetrates the cuticle of the host and sends a fine tube into a cell of the surface layer of the leaf, where it swells out and forms a haustorium, usually more complicated in structure than he haustorium of a rust. These

haustoria in the epidermal cells are the only source of food for the fungus, all the hyphae of which grow on the surface of the host. As soon as it has established itself it begins to form stiff upgrowing hyphae whose tips, as shown in fig. 33*a*, cut off in succession a chain of spores called oidia, which are the main means of dissemination of the fungus; they contain one nucleus each. In the autumn the mildew begins to produce minute ascocarps (figs. 33*b*, *c*), which are usually dark coloured and up to 1/100 of an inch across, usually smaller. They contain a small number of asci, and are the only part of the fungus possessing binucleate cells; this is usual among Ascomycetes, and in the present case may account for the relatively less complicated specialization of the mildews compared with the rusts. Each ascus forms eight spores, which are liberated in the spring, after the ascocarp, like the teleutospore of the rust, has had several months to prepare; from this point the cycle begins afresh.

The relatively restricted damage caused by the mildews is due not so much to chemical specialization, though this plays a part, as to their mode of life, which affects only the surface of the host. On the whole mildews are less important to man than rusts are, but a few, such as the kind which attacks vines, are able in time to kill the plant, and others such as the American gooseberry mildew are serious because they spoil the look of the food offered for sale; here the very character which renders the mildew biologically innocuous is responsible for its being socially a pest.

Besides these two important groups of fungi, there are several others which are in some degree comparable with them in their habits; but as this is not intended to be a treatise on plant diseases, it would be better if we were to pass on to consider the means by which these diseases are combatted, and then we shall describe the importance of fungi in other branches of industry.

CHAPTER X

CROP HYGIENE

EXCEPT for a few rare and ornamental trees, few plants are individually so valuable as to merit the time and trouble required to cure them of a disease. Thus in the study of plant disease it happens, as it ought to have done for other reasons in human medicine, that prevention is more regarded than cure.

The aim of the farmer or fruit-grower, in this matter, is to make his crops immune or partly immune to the attacks of fungi (and insects, but that is another matter); to do this, three avenues are open. First and most effective he may select varieties which have a congenital resistance against infection by a particular disease; but in many cases no such varieties are known, or else they have poor qualities in other respects, so that the grower is prepared to grow better kinds and run the risk of their being blighted. Failing that he may, as a second alternative, make his crops artificially resistant by covering them with some fungicide which will kill any spore which alights on their leaves; however there are many crops from which the expected profit is too small to make it worth while to do this. Even so the careful farmer may take steps in the management of his farm so as to minimize the possibility of any disease which may be about getting a serious foothold.

The breeding of plants so as to combine disease resistance with reasonable standards of quality is the concern of the geneticist and the plant breeder, and is properly outside the scope of this book; nevertheless, a few remarks may be interesting. The procedure has many limitations, one of them being that true inheritable immunity to the less exact-

ing and more destructive kinds of parasites is rarely found. Potato blight, for example, certainly attacks some varieties more than others, but none are truly immune. On the other hand, against wart disease, caused by *Synchytrium endobioticum* (a lowly fungus but a very specialized parasite) there do exist immune varieties, which are the ones most commonly grown today. The difficulties of breeding for resistance to rust have already been referred to, and these are enhanced by the need to include all the other qualities desired for agricultural purposes in the characteristics of the new varieties. Among the most successful plant breeders have been the Russians, who have among other things taken pains to secure wild strains and wild species related to the important cultivated crops, to obtain from these the desired qualities of disease resistance.

The most important method of combatting crop diseases is by means of fungicides; usually the aim of destroying insect pests, which requires much the same methods, is combined with that of preventing fungus attack, and the custom common to most universities of studying insects and fungi in separate buildings has probably a retarding effect on both fungicide and insecticide development. Pesticide treatments may be applied to the soil, the seeds, or the growing plants. Some expensive plants may be grown in soil sterilized by steam, but usually such attempts as are made to disinfect the soil (and they are not yet widely practicable) are by treating it with chemicals. Crops which are started in seed beds, such as lettuces, are often attacked by fungi which specialize in the killing of young plants, such as *Pythium deBaryanum*, and in such cases soil sterilization may be a practicable method.

Against most seedling diseases, and fungi whose spores are carried on the surface of the seed, dusting the seeds with protective compounds is the most effective method; the substances most commonly used are organic compounds of

the metal mercury, and cuprous oxide. Mercurials are sometimes toxic to the plants, and harm them as much as the fungi would do, while not every kind of fungus is killed by the cuprous oxide; indeed there are no fungicides of any kind which are quite free of harm to the plant and at the same time kill every species of fungi. Against the kind of parasite which is carried *inside* the seed, like the loose smut of barley, dusting with fungicides is of no use; it is necessary to heat the seeds in hot water, which must be very carefully done so as to kill the fungi without spoiling the seed; even so the treatment is not entirely satisfactory, and the best precaution against this kind of disease is to sow only seed known to come from a healthy crop. Grain which carries loose smut hyphae in it is quite fit for food for men or animals.

Most diseases attack plants when they are fully grown, though in nature at least the greatest number of casualties is certainly in the seedling stage. Herbacious plants are especially subject to leaf and root diseases, but trees are infected sometimes *via* the bark. Leaf diseases are combatted by spraying the tree or crop with a fungicide suspended in water (or sometimes dissolved in oil) or an emulsion of oil and water. It is necessary to make a given quantity of the active material (which is always the most expensive ingredient) go as far and last as long as possible, and it must therefore be spread thinly and made to stick fast to the leaves. This can be done in part by spraying the liquid very forcefully onto the trees, but it is also necessary to put into the mixture something that will make the little drops spread as widely as possible over the surface (called a spreader) and another to make the dried deposit stick (called a sticker) even when washed by rain. In order to encompass all these objects, to which effectiveness against insects may be added, fungicidal sprays are usually very complicated mixtures, of which only one or two constituents are active against the

fungi. The most common substances used for this purpose are sulphur and its compounds, compounds of metals, mainly copper, and organic compounds of various kinds, mostly those called phenols. Mercury compounds though more active against the fungi are mostly too expensive for use in sprays and often harm the plants.

34. PREVENTION OF DISEASE
Tomatoes being dusted with lime-sulphur as a fungicidal treatment.

Instead of spraying, which requires rather elaborate equipment, the fungicide is sometimes applied by dusting (see fig. 34). This method is said to have been first used by the French vine growers, who used flowers of sulphur to combat the mildew referred to in the last chapter, though lime and other substances were used as seed treatments in England in the eighteenth century. It was also in viticulture that the first spraying method was developed (partly by accident) namely the use of Bordeaux mixture, which is made by adding copper sulphate solution to slaked lime, and is still, curiously enough, one of the most effective fungi-

cides known. Against insect pests the Americans sometimes *fumigate* quite large trees, building tents over them for the purpose, and the same treatment has some effect against fungi but it is not at all permanent. Fumigation of glass-houses is of course a common practice, and is also used against mildew and some other leaf diseases, plain sulphur being here also an early and quite effective substance to use. A third alternative to spraying is to apply a fungicidal paint with a brush; this is done when a branch of a tree has had to be cut off because of a disease of the bark or wood, in order to prevent wound parasites from getting a foothold in the freshly exposed stump. Many orchard growers nowadays paint over the scars left in pruning, with the same end in view.

Root diseases are usually the most troublesome to deal with. Sometimes disinfectants applied to the soil give good results, but usually this method is too expensive, and the main way of preventing root disease is by what is called crop hygiene. By this is meant the proper management of a farm or garden, so that the opportunities offered to parasitic fungi (and insects), which are necessarily greater than those open to them in non-human environments, shall be as few as possible. For example the brown rot of apples is caused by *Sclerotinia fructigena* which lives during the winter in a dormant condition in rotten fruit; if all the dead fruit is collected and burnt after picking, there will be far fewer spores available in the spring to start a new attack; and if all growers were effectually persuaded to do the same, there might be a substantial reduction in the incidence of the disease.

Again, in relation to root diseases, allowing the soil to retain, unnecessarily, dead stumps or pieces of dead wood, may enable root parasites to keep going and preserve a source of infection, where otherwise they would die out. In the cultivation of tea *Armillariella mellea*, the honey-

fungus which is a common toadstool also in this country, is a serious root parasite. It can be killed out if the trees on which it naturally grows are ringed by a cut round the bark some months before they are felled. If this is not done the fungus lives in the dead stumps, which it is expensive to remove, and attacks the tea bushes when they are planted. It is also important wherever possible to prevent the fungus forming spores. For example *Stereum purpureum* is a parasite in plum trees causing the disease called silver-leaf, but it is only on dead wood that it produces its perfect stage (which is a small greyish bracket-fungus). If all the dead wood is removed by midsummer, no spores can be produced that year, and the spread of the disease will then depend on fungi growing wild in the woods.

Not nearly enough is known about fungi, or about their ability to damage our crops, for us to claim that their pestilential activities could at present be stopped altogether; they could certainly be reduced substantially if all farmers could afford to take due measures of crop hygiene, and the yield of our fields could be increased by the judicious use of fungicides. And if this branch of research were conducted more extensively, on a world scale, the food producing capacity of the world could soon be made to exceed the demand.

CHAPTER XI

WE HAVE THEM TOO

It is not only plants that are subject to attack by fungi; other fungi are often smitten with fungus diseases, like the Amanita in fig. 35, which is attacked by one of the Phycomycetes described in Chapter XV. There are also several families of fungi which have taken to living parasitically on animals, including man.

The diseases called dermatomycoses in medical science are caused by microscopic fungi belonging mostly to the Ascomycetes, and resembling the yeasts described in Chapter XIII; research on them has been hampered in the past by the fact that mycologists do not enter into medical research, whereas medical students are expected to acquire only a superficial knowledge of fungi; thus, like many other borderline sciences, the study of the dermatomycoses suffers from having too few competent investigators. There is certainly much to learn about the fungi which cause them, though their relative degree of importance in various countries is fairly well known.

Most of the fungi involved are very untypical specimens of their class, because of the very unusual mode of life they have adopted. This is a case of a general rule in biology, that organisms which in the course of evolution have taken up a manner of life very different from that of their ancestors tend in the course of many ages to become outwardly more like unrelated species which have the same habitat than their own relatives, though it is generally not beyond the powers of careful investigation to reveal their true nature. In addition to the true fungi, there are a few diseases caused by Actinomycetes, which are a class of organisms sometimes

counted as fungi, though they are probably in fact much closer to the bacteria. Like fungi they consist of a network of fine threads, but they are much narrower than those of most fungi, and their only method of reproduction is the breaking up of these threads into little rod-shaped bodies,

35. A DISEASE OF A FUNGUS, CAUSED BY A FUNGUS
A species of *Sporodinia* attacking and killing *Amatnita rubescens.*

indistinguishable by themselves from bacteria. There is a fairly common disease of cattle, called "wooden-tongue" caused by one of these, and it is said sometimes to attack man, A few plant diseases are due to them also, but the great majority of species live harmlessly in the soil.

The diseases caused by true fungi are nearly all diseases of the skin, probably because the fungi have little chance of getting at the internal tissues. They are apt to be difficult to treat, partly because it is easier to find ways of killing bacteria without poisoning the patient, than it is to discrim-

inate between man and fungi. On the other hand they are relatively easy to prevent, regular washing being a sufficient precaution in most cases; that is because the fungus spores, which are the germs of the disease, require (as in the case of plant diseases) to be left in position for some time before they can establish themselves. Perhaps one of the reasons why so few fungi have taken to attacking mammals is that the body temperature is too high for them; most of the commonest fungus diseases occur on the more exposed parts of the body, which are cooler, and fish and other cold-blooded animals are much more subject to them than we are.

One of the chief factors favouring the spread of diseases of this kind, as of others, is overcrowding, which enables the spores to be carried more easily from one person to another. Also, of course, overcrowded housing conditions make it harder to keep clean. The majority of these dermatomycoses must therefore be classed as preventible, within a measurable time, in civilized countries; and they could in principle be abolished altogether from the world, as they no doubt will be when the economic causes of bad living conditions can be eradicated on a world scale.

A typical example of one of this class of diseases is "ringworm". This has as its chief symptom the appearance on the skin of red marks, in the shape of little rings, often incomplete, and when they appear on parts that grow hair, the hair falls out; they are commonest on the scalp. As time goes on they increase in size, and when they meet, the boundary region disappears, behaving in exactly the same way as fairy rings (see fig. 2*e*, p. 13). In fact they *are* fairy rings, being produced by just the same cycle of events, except that the cause of ringworm is a minute microscopic fungus and not at all like a toadstool. Of course, the red colour is not the colour of the fungus, any more than is the green colour of the rings in our fields, but is an inflammation produced by the fungus in the skin.

Another skin disease due to a fungus is called "Trench foot". It first came into prominence during the first world war, when it was common among the soldiers who had to spend long periods in the trenches, whence the name. But it is also met with in all the less civilized parts of the world, being known by different names in different places. Here too the basic cause is unhygienic conditions, but since permanent wet feet are a form of discomfort which most people will do a lot to avoid, it is not very common under ordinary circumstances. In this case the fungus does not form fairy rings; the chief effect is a swelling and inflammation of the skin, and the disease can be very painful.

As already mentioned, most of the fungi that cause skin diseases are yeast-like, in that they do not form hyphae like other fungi, but appear as separate cells. However, many kinds of fungi will take on this appearance when growing under unfavourable conditions, so we cannot infer that these "dermatomycetes" are really related to the yeasts, though it is believed that some of them are so. Some skin fungi, moreover, form typical hyphae even in their natural habitat.

While on this subject, we may remark on one very common disease which may be caused by fungi, and cannot be prevented by washing. I refer to hay fever. This is due to an individual idiosyncrasy making the patient intolerant of some particular substance, usually if not always a protein. The commonest provoking cause is the pollen of plants, especially those that rely on wind to effect fertilization rather than insects, because these produce much greater quantities of it; but among less frequent causes (at least it is believed that it is a less frequent cause) is the spores of fungi. Owing to the great number of spores produced the air is always fairly well stocked with them, and unlike those allergic to pollen the sufferers from this variety of the disease do not find their troubles confined to one season of the year.

Some fungi have a more specific effect, which may be

due to their growing on or in the body, but is more likely to be a special sort of allergic response. Such a one is *Aspergillus fumigatus*, the spores of which if inhaled may cause symptoms resembling tuberculosis; fortunately it is not a common mould. I have myself been exposed to quite a lot of it without ill-effect.

On the whole, we must conclude that, as direct causes of disease to man, fungi are of relatively little importance compared to bacteria and one-celled animals, and that this mode of action accounts for but a very small fraction of the damage they do to us.

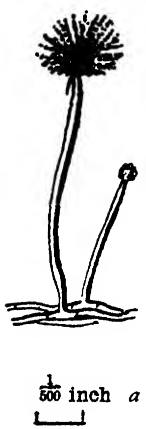
CHAPTER XII

ON GOING MOULDY

AFTER the kinds which attack our crops as parasites, the fungi most damaging to man's social products are those which spoil and destroy manufactured goods. A considerable variety of materials are liable to "go mouldy", of which wood (and everything made from wood), cotton and other textiles are the most commonly affected. Going mouldy is always the work of fungi; this is hardly surprising, because it is but one more manifestation of their primitive and original way of life, that of disposing of the dead remains of vegetable matter. When men try to preserve what is, in nature, ready to be destroyed, they naturally come into conflict with the natural agents of that destruction.

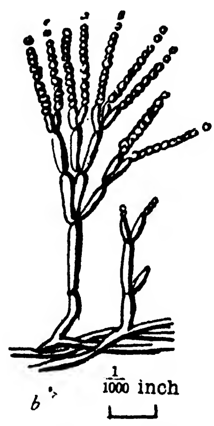
If you look around in a lumber room or garden shed, you will usually come across some piece of leather or cardboard which is "mouldy". It has green or grey stains on it, and if the stains are touched with the fingers, they are usually found to be of a dusty consistency, though they usually cannot be altogether rubbed out. The dusty material is the spores of the fungus, and the cause of the stain is the mycelium, which grows in or on the material. The great majority of cases of mouldiness are caused by members of a single family of fungi, called the *Aspergillacei*. These are Ascomycetes, though most of them have lost the power of producing asci, and reproduce entirely by means of their very abundant dusty "conidia"; in fact, these were the first fungus spores to get the name of conidia, which means "dust-bodies". These conidia are formed in long chains (rather like the chains of oidia produced by the mildews) which grow in tufts often resembling an artists brush or the

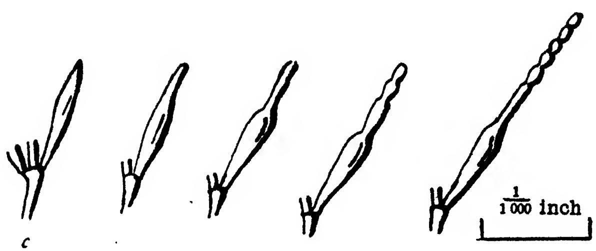
head of a mop. (See figs. 36*a*, *b*). The chains are formed by the appearance of a series of constrictions towards the tip of a special hypha (see fig. 36*c*). These constrictions are formed one behind the other, while the undivided part of the hypha continues to grow. After the spore has been completely nipped off it is only held to its neighbours by a light adhesion, so that the least breath of air breaks up the chain and scatters the tiny spores, which are no more than a few ten-thousandths of an inch long. As in nearly all the Ascomycetes there is only one nucleus in each conidium, and only one in each cell into which the hyphae are divided.



36. MOULDS

a. a young and mature conidiophore of *Aspergillus niger.*
b. a conidiophore of a species of *Penicillium.*
c. five stages in the development of spores in *Poecilomyces varioti.*
d. ascospores of *Aspergillus amstelodami;* note the pulley-wheel shape.





I mentioned in the last chapter that the air is always full of fungus spores; of these something like 90 %, sometimes even more, are of the *Aspergillacei.* In ordinary town air you take in a dozen or more with every breath, and most

likely get a few even at sea; this means, apart from the possibility already mentioned of ones being allergic to them, that there is very little chance that any object on which these fungi can grow will escape infection, unless very special precautions are taken.

As one would expect, seeing how easily these spores can be carried in the upper air, most of the common moulds are of world-wide distribution. But it is in tropical countries that they do the most damage, because the warm temperatures and moist airs of such regions are especially favourable to their growth; indeed the Aspergillacei may be counted among the great enemies of society in such climates. The temperatures most favourable to the growth of moulds are around 80 to 90° F, and for them to form spores the air must be nearly saturated with moisture. In such countries as coastal West Africa, Malaya, and New Guinea, these conditions obtain most of the year round.

If a spore of a suitable kind lands on almost any kind of organic substance (and we can take it for granted that there always will be a spore handy), a vigorous growth will be made. Practically every organic material found in nature, or chemically similar to such, may be attacked. Apart from the look of the thing, this may not do much harm, but there are moulds able to rot away the fibres of cotton or rayon, while others can destroy the protein fibres, namely wool and silk. Even without causing mechanical destruction, they may do grave damage. Thus during the second world war many lives were lost in tropical campaigns through radio sets being put out of action by moulds growing in them and causing short-circuiting and other electrical faults. Even the lenses of cameras and field-glasses are liable to go mouldy sufficiently to render them unusable.

One naturally asks, What can be done about it? The answer is that the best way of foiling the disposers of organic remains is not to use organic remains for essential purposes,

at least not until they have been made unrecognizable to the moulds. A few years ago this advice would hardly have been practicable, because men have always relied almost entirely on other organisms for their materials, other than pottery, stone, and metals. None of these three things go mouldy (though fungi can cause iron and copper to rust if they grow in contact with them), but not everything necessary to civilized life can be made from them: wood is indispensible, and clothing (to mention only two items) has always been taken from the organic world. Nowadays however we are in position to replace most of the organic substances used by man, except wood for building, by synthetic materials which bear no chemical resemblance to the natural food of fungi. The cellulose plastics, and synthetic fibres such as rayon, which are made from wood pulp or cotton waste, are still near enough to their original from to be palatable to moulds, but most of the more recently invented plastics are as mouldproof as a china cup, unless (as is often done) natural products such as castor oil are incorporated in their manufacture.

Natural rubber is fairly mould-resistant, but manufactured articles, unless vulcanized, are less so; the better grades of vulcanized and synthetic rubbers are not liable to grow moulds. Among synthetic fibres nylon is almost immune from fungus attack. However, wide as the range of these synthetics now is, we cannot get away entirely from wood and its products; even if it were economic to do so it would be unwise, because most manufactured plastics come from coal, which is limited, whereas wood need never be lacking from the Earth.

To make natural products mould-proof, we have to treat them with fungicides. This is definitely less effective than the use of materials inherently unsuitable for fungi to grow on, but it is possible to preserve wood fairly well. Some tropical woods, such as ebony, are in their natural state

impregnated with substances which protect them, and this is itself an adaptation acquired by the trees, through natural selection of those best able to withstand fungus attack. Teak is also resistant, and abundant enough to use for building on a small scale. But most kinds of wood need some kind of treatment, even in temperate climates, and of these the creosote bath, given to telegraph poles and wooden huts, is one of the best; the preservative solution has to be forced into the wood under pressure. Unlike paper and textiles, structural woodwork needs protection mainly against toadstools and bracket-fungi belonging to the Basidiomycetes, which are in any case more slowly-growing organisms.

The protection of paper is a more difficult problem. Fungicidal treatments usually spoil the paper for writing on, and to avoid that and at the same time to keep moulds away is very difficult. One of the best ideas yet tried is to impregnate the paper with synthetic resins, but ultimately the solution will probably be to use, in tropical climates, an all-synthetic substitute, which we have not yet discovered.

Not only boots and paper and radio sets go mouldy, but, as every housewife knows, food is also affected. To protect food from moulds it is little use adding fungicides, because these are nearly always as poisonous to men as to fungi, nor does the digestion welcome the use of synthetic substitutes. There is however one preservative which is effective, and that is sugar. This is perhaps surprising when we consider that all food moulds thrive better on sugar than anything. The reason is that if the sugar is sufficiently concentrated it has a greater attraction for water than have the fungus hyphae, so that they cannot get the water they need out of the jam, and the sugar is no substitute for that. That is why if you make jam with too little sugar, as is often done nowadays, you have to eat it quickly; fungi can grow on it because there is too much water in proportion to the sugar.

More generally effective as a means of preserving food

is to keep it where there are no spores of fungi to infect it. When you bottle fruit, what you do is to kill the fungus spores and other micro-organisms that are already there by boiling it, and then quickly seal it up tight so that fresh spores can not get in; it is remarkable how few of those who use this technique understand the reasons for what they do. The same thing is done in factories where food is packed in tins. Finally for those kinds of food which cannot be tinned or bottled, or for the sake of avoiding the loss in quality inseparable from this kind of treatment, one can keep the moulds from growing by storing it where there is no oxygen, or too much carbon dioxide, or at too low a temperature for the organisms to live. We must however remember that most food spoilage is caused not by fungi but by insects, such as the bluebottle, or bacteria.

CHAPTER XIII

AT YOUR SERVICE

ALTHOUGH, as explained in the last chapter, the family of the Aspergillacei are the chief cause of mouldiness in paper, textiles, and leather goods, they are also one of the most profitable families of the fungus world for human industry. The good as well as the harm they do are both due to the exceptional variety of chemical substances which these fungi are able to make. All fungi, as compared with animals or plants, are distinguished for chemical versatility, being able to make (or to acquire the power to make) a greater range of chemicals, and thereby attack a greater variety of substances, than the organisms which make their own food or have the power to search for it. This character is necessary to them in their mode of life as refuse destroyers, and is shared also by the most primitive existing organisms, the bacteria. But it seems that the Aspergillacei have been particularly successful in this, and by growing them on suitable nutrients it is possible to get out of the liquid they have used a variety of chemicals which it is otherwise difficult or impossible for us to make. Some of these are produced in large quantities, but are relatively simple chemicals, such as citric acid, while others, more complicated, are produced in minute quantities.

Most of the simple chemicals thus obtained, which are also of use in industry, can be obtained more cheaply by other means, starting from coal or limestone; but it happens that in the case of citric acid that the method of getting it from fungi can compete commercially with synthetic processes, and with lemons which were the original source. As to the complex compounds which the moulds produce

in very small amounts, we shall not for a long time know them all or understand their properties; but some at least, because of their usefulness and because we cannot yet make them synthetically, are worth growing the moulds for.

More than ten years ago some bacteriologists, working with Prof. Florey at Oxford, and following up an earlier observation of Prof. Fleming, found that when they tried to grow various bacteria, causing disease in men and animals, in pure culture, and accidentally got some mould spores mixed up with them (a thing very easy to do because of the great abundance and small size of the spores) the bacterial cells were killed near where the mould was growing. This hint was pursued, and it was soon found by Prof. Florey's team that certain moulds, and particularly a certain strain of *Penicillium notatum*, produced in the course of their growth a definite substance able to kill bacteria of certain kinds. The problem was then taken up by the chemists, who were at length able to separate, from the liquid on which this mould had been growing, a distinctive crystalline material possessing a very strong poisonous action against a wide variety of bacteria, and at the same time having little or no effect on animals; this they called penicillin. The possibilities of such a material in medicine were obvious, especially in time of war, and the next stage was to hand it over to the doctors to see if it was any good in practice; for many substances, apparently suitable in the laboratory, turn out to be no good as medicines. It may be that they kill bacteria in a test-tube, but not in a man's blood, or they may be too quickly destroyed in the body by some chemical reaction.

This turned out to be the trouble with penicillin; it would only last a few hours in the body, and so had to administered continually. However it was so good in other respects, that they persevered, and evolved methods of getting over the trouble. It was found that penicillin was a cure for a sur-

prisingly wide variety of diseases; to read a list of them reminds one of the optimistic writings of the mediaeval herbalists, who were prone to believe anything of a herb they had not themselves tried; but in this case the reports are true. Of course, it is not all on the good side; even of those diseases which are caused by bacteria, which are by no means all, some do not respond to penicillin treatment. Again, the chemical instability of penicillin makes it difficult to store. Some of these difficulties will no doubt be overcome, others will not, but at any rate it is safe to say that it is already one of the most important drugs now available for a number of diseases, such as pneumonia, syphilis, and the treatment of wounds.

It is made by a rather elaborate process of extraction from the solution on which *Penicillium notatum* has been grown; the temperature, composition of the solution, and time of growth have to be carefully adjusted to get the best yield, and there is still room for improvement both in the extraction methods and in the strain of fungus used. It is not certain that it will go on being economical to get penicillin from its natural source, because the chemists now know its structure and are trying to find out means of synthesizing if from cheap raw materials, though this is expected to be a difficult project, and it may be a long time before success is reached. If so, it will be worth while to breed new strains of fungus for increased penicillin production; for the amount of drug produced from a large amount of mould is at present very small, and the overhead costs of production are correspondingly heavy. However the task of breeding *Penicillium notatum* will also be surrounded with difficulties, because the fungus does not reproduce sexually (as far as we know) so that hybridization will not be possible.

One by-product of the discovery of penicillin has been a sudden increase in interest in fungi in general as possible sources of useful chemicals. As already mentioned, one of

their characteristics is a considerable versatility in chemical matters, and it is thus good to look to these organisms for new ideas; furthermore if, more or less by accident, we have stumbled across so valuable a substance as penicillin, we may hope to get something still better by ordered search. Such searching is now going on, and quite a number of substances able to kill disease-causing bacteria have been found; so far, nothing so good as penicillin has come to light, but there is at least one product which, in laboratory tests, kills bacteria of kinds immune to penicillin; this one, called Streptomycin, is produced not by a fungus, but by one of the Actinomycetes referred to in Chapter X. Streptomycin is already in use in medicine, but it may prove to have some drawback which makes it only of limited value; it is never safe to prophesy in such matters.

Earlier than the use of moulds to produce drugs the mediaeval doctors had thought highly of certain toadstools, and other higher fungi, as medicines. Several of them are emetics, causing sickness, which is quite a useful property, though there are plenty of better things for the same purpose. A small brown toadstool which grows on wood and is very common, called *Panus stipticus*, was used to staunch bleeding; but the virtues of most fungal remedies were (like many others) purely imaginary. However the toadstools are now being systematically examined for medicinal products, though without any great success so far.

The exploitation of mould fungi for their more abundant products, which can somtimes be obtained in considerable quantity, has naturally been going on for longer. The most important substance obtained in this way is, as already mentioned, citric acid. Although this acid, which is used chiefly in the confectionery and soft drinks industries, can be produced from simple raw materials such as vinegar, this process cannot compete commercially with its extraction from natural sources. Lemons were the original source,

and are still largely used, but an increasing quantity is extracted (by a much simpler process than that used for penicillin) from the solution on which moulds have been grown. The species most used are the common black mould *Aspergillus niger*, and various species of *Penicillium.*

Here again there is much scope for improvement in the productiveness of the fungi employed, by breeding and selection, but, as in the case of penicillin, there is the difficulty that they do not produce asci, and thus are not able to be hybridized; for the essential step in hybridization involves the fusion of the two nuclei, derived from different parents, and this occurs in the life cycle of the Ascomycetes only in the developing ascus; when the mould cuts out the ascus stage, as these do, hybridization is impossible, and breeding is correspondingly slow. Such fungi have by this reduced their own ability to adapt themselves to changes in their environment, and are therefore probably ultimately destined to extinction unless preserved by human care; but that will take many millions of years.

Useful as the Aspergillacei are to present day society, it is not these moulds, but fungi of even simpler structure, that have contributed most extensively to human welfare. These are the yeasts and to these we shall now turn.

CHAPTER XIV

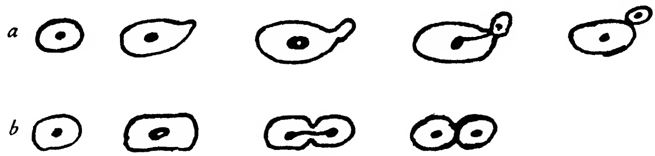
BREAD AND WINE

LONG before anyone had thought of using mould fungi for industrial purposes, perhaps even before they had tried to use toadstools as medicines, men had domesticated at least one species of fungus, and used it to good effect in their daily lives. This is known nowadays as yeast, or in scientific language *Saccharomyces cerevisiae;* but other species or the Saccharomycetacei and closely related families may have been early in use, and are certainly employed today.

Considering how long the yeasts have been in use, it is rather surprising how little their true nature has been understood; even their recognition as living organisms had to wait on the invention of the microscope and was only confirmed by Pasteur's researches which disproved the possibility of their spontaneous generation. Yet its ability of increase itself, which we now regard as one of the most characteristic properties of life, was the thing which the ancients were most struck by in the behaviour of yeast. Nowadays we not only know that they are microscopic fungi, but can classify them among the Ascomycetes; it is true that not all kinds are certainly known to belong to this group, and there is one family, of no economic importance,* which are Basidiomycetes, but these are usually excluded from the "true" yeasts. The chief characteristic by which yeasts are distinguished from other fungi is by their failure to form hyphae. A typical yeast consists of a large number of roundish or egg-shaped cells, attached to one another in small groups, but with no tendency to form those long threads

* There are some species which are a minor cause of spoilage of paper in the tropics.

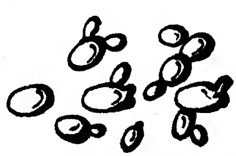
of which the mycelium of a toadstool, for example, is built up. The little groups of cells are formed, typically, by a process of budding, as illustrated in fig. 37*a*. There is another family, however, called by the regrettable name Schizosaccharomycetacei, in which the cells divide by fission into equal parts, as shown in fig. 37*b*, but these likewise fail to form hyphae.



37. THE DIVISION OF YEAST CELLS
a. budding, typical of most yeasts.
b. fission, typical of the Schizosaccharomycetacei.

This budding habit is by no means confined to the yeasts properly so called, but is exhibited by various fungi, though usually only under conditions of restricted food supply. In the yeasts however it has become the normal habit, though there are some species which can be induced to form short hyphae by growing them under carefully controlled conditions. In fact the yeasts are not, as was once thought, primitive one-celled fungi, in the same way that most of the unicellular animals and plants are primitive representatives of their respective types, but are descended from ancestors having the typical hyphal habit; intermediate forms still exist. An illustration of the type of growth produced by typical yeasts is given in fig. 38.

This we must count as a degenerative change, such as is very frequent among the evolutionary lines of fungi; it is almost certainly related to their mode of life. In nature the yeasts have specialized in what is chemically the easiest



38. A GROUP OF CELLS OF BREWER'S YEAST

possible expedient, that of using starch and sugar as their chief foods. Some insects produce sugary secretions (so called "honey dew") and most flowers produce nectar which is mainly a solution of sugar in water, which attracts insects and so aids in pollination; a similar secretion is induced, as we have seen, by rusts, on certain plants that they attack. All these natural sources of sugar have been exploited by various families of fungi, and of these the most successful have been the yeasts; they are, despite their much simplified structure, not without specializations for this way of life, for they can often derive nourishment from solutions of sugar so strong that other fungi cannot use them, for reasons explained in Chapter XI. But sugars of various kinds can be obtained also by chemical breaking down of starch, which is a good deal commoner in nature than sugar itself, and probably the starch in dead plant remains is the chief means of subsistence of wild yeasts. Man very early learnt where to find sources of sugar and being, like other animals, very fond of it, frequently laid up stores of honey and other sugary things, and these must often have been infected by yeasts. Now if there is plenty of air available yeast changes sugar in the same way as if it were burnt, into carbon dioxide and water (this is also the ultimate fate of sugar in our bodies). But if the air is excluded (as would happen if they kept their sweet juice in a closed jar), the chief products of the yeast's activity are carbon dioxide and alcohol. Thus it might easily happen that an alcoholic drink was produced by accident. Then if, to reproduce the pleasant effects of this, the makers of it had relied on the usual magical practice of adding a little of the potent liquor to the next brew, the latter would (as expected) acquire the "spirit" of the former, and the first mycological technique would have been discovered.

There is one difficulty about this process, and that is that the yeast cannot grow if the concentration of alcohol exceeds a certain maximum, so that there is a limit to the

potency of the beverages thus obtainable; really strong drink has to be made by distillation from the natural product. Almost any vegetable matter can be used as a source of alcohol by the help of yeasts, but those used for drinks have most usually been plants also used as staple foods. The Oriental peoples brew liquor from rice, the Western nations prefer cereals such as barley or rye, or even potatoes; fruits, because of their greater sugar content, have always been favourite materials for this process, of which grapes have taken first place both in East and West, and for the same reason the brewing of honey and molasses, giving mead and rum (the latter is distilled) is almost coterminous with knowledge of these commodities.

But whereas in the past the use of yeast has mainly been to produce the means of drowning the sorrows of life, which in earlier ages were in general more grievous than now, the future is likely to reveal a new role for this fungus as a producer of alcohol for fuel. For this purpose it has the advantage over coal and oil, and even uranium, in being available in inexhaustible supply; though it may be that the Earth's capital resources of power will last us until still more convenient and abundant sources have been discovered.

Knowing the virtues of yeast in the improvement of drink, it was natural to the early civilizations, though at a more advanced stage of culture, to try its effect on solid food. Whatever early attempts may have been made in this direction, one which was sufficiently successful to survive was its use in baking. If flour is mixed with water it makes dough, and if dough is baked it goes hard, and if it is then eaten it is nutritive in principle but heavy on the stomach. If however a little yeast is added to the dough, and given time to act, it will decompose part of the starch which is its main constituent and, producing carbon dioxide as a by-product, will leaven (that is, lighten) the mass with the bubbles of this gas, so that when the bread is baked it will

be both more palatable and more digestible. It will also produce a little alcohol, but this is volatile and is thus largely driven off during the baking, so that the finished bread contains very little of it. Thus the usefulness of yeast in baking depends on a different principle from its value for brewing.

Those pastoral peoples who first took to the use of animals' milk for human consumption early discovered ways and means of turning it into different forms. Various methods of making milk turn sour have been invented, and many of them involve the use of yeasts. In some cases the yeasts are mixed with other organisms, mainly bacteria and sometimes other fungi, in such proportions that the mixture produces its various enzymes, by which it decomposes the milk, in just the right ratio to ensure the reproduction of all the constituents of the mixture at the same rate. In such cases the mixture behaves in some ways like a single organism, just as a lichen behaves not like two organisms, fungus and alga, growing together, but like a single one. It is in fact an interesting case of symbiosis. One such mixture is known as "Palestine Bees"; these are little lumps containing yeasts and bacteria of at least 3 different species which, when put into sugared milk, ferment it. As they do so they grow, and at length, owing to the accumulation of carbon dioxide inside them, break up into smaller pieces, thereby simulating the cycle of growth and division of a true organism. Another example is the "ginger beer plant" which makes ginger beer from sugar, water and ginger.

Yeasts, again in association with bacteria, are also very important in the making of cheese; in the later stages of this process other fungi, particularly certain species of *Penicillium*, play a part especially in the green cheeses, to which they give their distinctive colour.

Apart from their auxiliary value in improving the flavour and quality of food, yeast fungi are beginning to play a

part as the substance of food. Yeast contains most of the chief requirements of a balanced diet, and is particularly rich in some of the minor food substances such as the B vitamins and phosphates. Various yeast preparations are now marketed as flavourings, and the production of food yeasts is an industry of growing importance, for example in the West Indies. But it is unlikely that, even though it is probably possible physiologically, any nation will take to using yeast as a staple food; it would be a rather monotonous diet.

All things considered there can be few organisms more useful to man than the Saccharomycetacei, and few fungi less harmful to his social products. And if it be protested that the use of alcoholic drinks is deleterious, the blame ought not to attach to the fungus; at any rate, few would hold that bread is an abomination. However, it has been suggested that the leavening of bread is one of the main causes for the dental troubles which now afflict civilized communities, since the greater toughness of the natural food both promotes full development of the jaw and prevents accumulation of carbohydrates in the teeth.

CHAPTER XV

FOOD AND POISON

PERHAPS the first thing which most people think of in connection with fungi is that some people eat some of them, but they themselves wouldn't dare to, because they are mostly dangerous poisons. It is generally believed either that one can distinguish poisonous from edible species by some simple test, or else that only "experts" can possibly distinguish any but the common mushroom. But in truth, quite apart from the use of lichens and yeasts as foods, which we have already mentioned, nearly all nations have taken to eating various of the larger fungi, mainly toadstools, and the incidence of fungus poisoning is never a serious social problem. It is certainly *not* true that the majority of species are deadly poisons, *nor* that the good kinds can be detected by rule-of-thumb methods, *nor* that *Agaricus campestris* * is easy to distinguish from possibly poisonous species, *nor* that all other kinds are hard to identify correctly.

It has been reported of the Fuegians that at one time *Cyttaria*, a large Ascomycete, was their staple food; but even if that is true it is probably the only case of any fungi affording the mainstay of life. But many nations partake far more widely of fungi than the Western Europeans, and may survive times of famine by their use; this was the case for example with the Byelorussians during the War of Intervention in Russia, where fungi are still eaten (outside the large towns) almost indiscriminately. However most European peoples observe various customary restrictions, commonly believing that all species which their customs forbid are poisonous.

* I avoid the word "mushroom" because it is liable to be misunderstood in in this context, as explained on p. 103. Anyway, the correct name for the species usually eaten in *Agaricus hortensis*.

This belief is commonly held by all primitive peoples concerning the foods which they themselves do not eat, and its survival in connection with fungi is probably due to these organisms being of little dietetic importance, so that little is gained by a more rational attitude to them. For in fact the nutritive value of fungi is low, though by no means zero; their dry matter consists largely of the material of the hyphal walls, which is very similar chemically to a lobster's shell, and this is probably indigestible (as is the cellulose in vegetables). Allowing 90% for water, certainly not more than 5% of the weight of the freshly gathered fungus "does you good", probably only 1 or 2%. Of this portion the most valuable food materials are the proteins, but fats are particularly low. Thus it is quite understandable that there has been little incentive to revise traditional beliefs about fungus food.

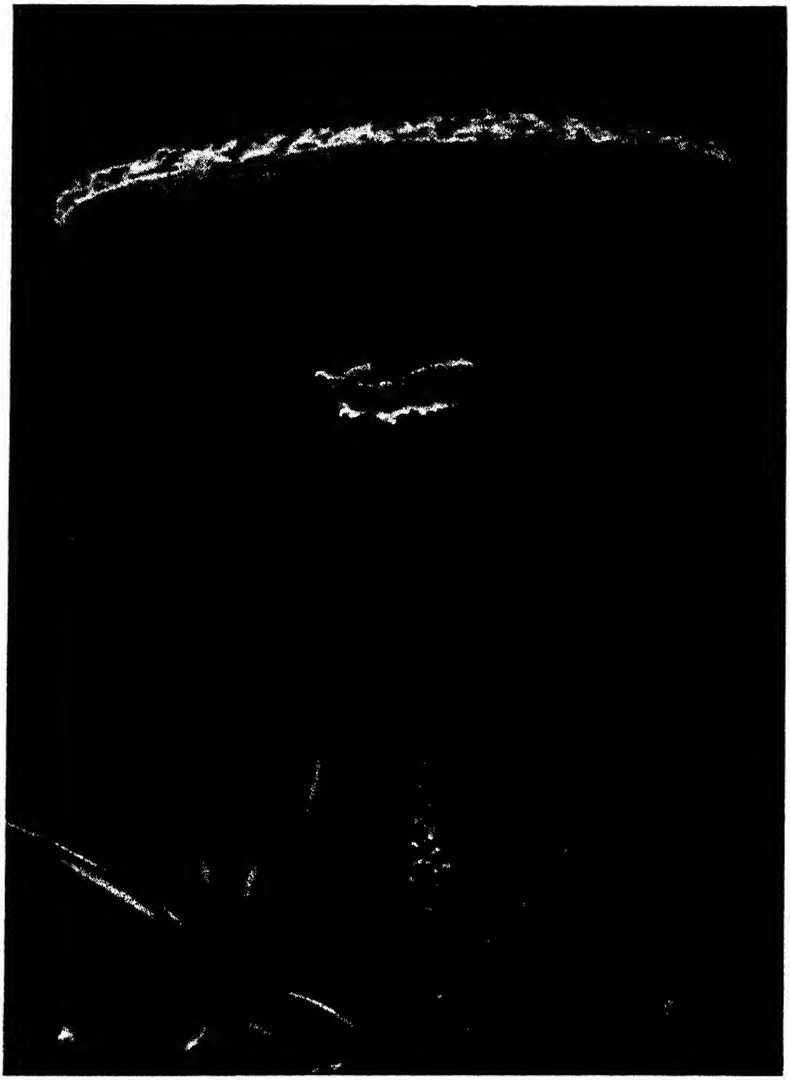
The truth about the poisonous properties of "toadstools" is that there are a few species, including the common *Amanita phalloides*, which are very poisonous indeed, and a considerable number which are emetics, and therefore unpleasant but not dangerous. There are a far greater number which are harmless, and of these several are sufficiently palatable to be worth collecting and cooking even when other food is abundant. The belief in the generally poisonous character of this kind of food has perhaps been sustained in Britain by our choice of *Agaricus campestris* as the one "edible" fungus. Almost everyone living in the country believes he can tell a mushroom from a toadstool; put to the test however there are four common species which most of such people will call mushrooms; one of these is *Agaricus xanthodermus*, which is definitely poisonous to some people, though not to everyone. Thus the public is fairly often exposed to the spectacle of people being sick after eating mushrooms, from which it is inferred that worse consequences might well follow their eating of toadstools.

The fact is that "experts" are never very confident of their ability to "tell a mushroom", and I have myself been asked about a doubtful specimen by a colleague, who yet consulted a third for confirmation.

Despite this difficulty, there is no doubt that our common mushroom is the most commonly eaten of all fungi; its spread has been conditioned by that of the horse, and it is probable that it is necessary for the spores to pass through the intestines of a horse before they will germinate. Nearly all nations that have long been acquainted with the horse eat mushrooms, but not all; it is said to be regarded as poisonous by the peasants in parts of France, and most Finns will not eat fungi at all. It is likely that mushrooms will grow less common as horses are replaced by tractors on our farms.

There are several common fungi found in Britain which are "safer" than the mushroom, and no less excellent to the taste. Some indeed, such a young puffballs (while still white inside), *Sparassis crispa*, which is a large spongy-looking mass of pale twisted branches growing on fir stumps, and *Lactarius deliciosus*, which has an orange-coloured milky juice, are quite unmistakeable by anyone. Next to the common mushroom the species most frequently eaten in this country are the parasol mushroom (*Lepiota procera* (fig. 39) and related species), the cep (*Boletus edulis*), and the blewitt (*Tricholoma personatum*) but all three have a purely local reputation. Any of the above species can easily be recognised by one who has seen them, and any reasonably intelligent person can learn to distinguish many other kinds, just as they can with hedgerow berries. No one intending to eat an unfamiliar fungus ought to rely on written descriptions, but if you can recognize the genus *Amanita* and avoid it, and always eat fungi cooked, you will be in no danger of death.

Naturally, the fungi which can be eaten have at various



39. AN EDIBLE TOADSTOOL
Lepiota procera.

times acquired economic importance; but their purposeful cultivation, as opposed to the gathering of them for sale, has been attempted commercially with only a very few

40. AN EDIBLE TOADSTOOL
Cantharellus cibarius.

41. A POISONOUS TOADSTOOL
Amanita muscaria.

species. One reason for this is doubtless the lack of incentive, due to their low food value, but it is a fact that the higher Basidiomycetes are very difficult to grow artificially, and success has often eluded mycologists even when they have sought no further than to grow one or two specimens in the laboratory. The easiest to cultivate (partly because they do not form mycorrhiza, which are certainly necessary for many woodland species) are those which grow on dung, of which *Agaricus hortensis* is one. Probably the ease with which it can be cultivated has been a major factor in spreading its popularity in Western countries, for civilized people always have more confidence in the grown than in the gathered. Mushroom growing is an important branch of food-production both in Europe and North America.

In Mediterranean countries truffles are "cultivated", or more properly speaking the oak trees with which they form mycorrhiza are tended so as to encourage the truffles. These are subterranean fungi belonging to the Ascomycetes, and though there are Basidiomycetes (related to the puffballs) of similar habit and appearance, they are regarded as much inferior by the gourmets. The truffles grow deep in the ground, and to find them it has been the custom in Normandy to train pigs, who find them by their scent; this was formerly practised in Wiltshire, but in this country the true Mediterranean truffle is not found. In Japan *Cortinellus shiitake* and related species are cultivated for food. Despite the technical difficulties involved, there should be scope for the cultivation of other edible species; for such advances we might look to the Russians, whose dietetic habits and economic institutions are both favourable to the enterprise.

As to the poisonous properties of fungi, we have already mentioned that popular belief tends to exaggerate them. It is of interest to note, however, that there is one poisonous fungus, namely *Amanita muscaria* (fig. 41), which was at one time used by the Kalmyks and other Siberian tribes,

for the sake of its intoxicating effects. The toxic principle is passed out, largely in its original state, in the urine, and this property is also said to have been exploited by these people. The effects are similar to those of alcohol, but more marked.

It is most important to understand that there is no "rule" for distinguishing edible from poisonous fungi. Very many people will freely cite such rules, but few (fortunately) act on them. The only rule is that if the specimen belongs to a species known to be edible, then it is not poisonous! In this country almost every case of fatal fungus poisoning is due to *Amanita phalloides;* it appears that those who eat it usually mistake it for the common mushroom, though the resemblance is very remote, and it may not be a coincidence that this species agrees with most of the supposed tests for edible kinds. It can be peeled, it does not blacken a silver spoon during cooking, it is commonly eaten by slugs, and it is rarely found, in the author's experience, near serpents' holes. Nor does it turn blue when broken, a striking property possessed by several esculent species of Boletacei, which have sponge-like tubes under the pileus instead of gills; this also is commonly cited as a warning sign. It should also be said that of many species it is not yet known whether they are poisonous or not. It is probable for example that *all* Boletacei are edible, but one or two species are still under suspicion. Here then is yet another interesting field for research; but it is likely that in the case of many doubtful species the explanation of the doubt lies in individual idiosyncrasy, as in the case of *Agaricus xanthodermus,* some people being susceptible and others not.

One group of poisonous fungi has not thus far been mentioned, because they stand in no danger of being confused with edible toadstools; of these, the most important is ergot. This is an Ascomycete, *Claviceps purpurea,* and it grows as a parasite on rye and some other grasses. Its habit is systemic

(that is, it grows through all the stem of the plant), and when the plant is ripe it grows into some of the developing ears, which it replaces by larger blackish horn-shaped bodies consisting of a dense mass of hyphae. These are shed with the grain, and when conditions are favourable, grow out into the perfect stage of the fungus on which the asci and spores are borne. The danger is that these "ergots" will be collected at harvest and mixed in with the grain. They are powerful poisons, but in very small doses they are useful as a drug, and at one time powdered ergot was much used to facilitate childbirth, and is still recognized in medicine. In countries where rye bread is a staple food there is an endemic disease caused by consumption of small quantities of ergot, and this is a serious problem. In Russia, where it was at one time very prevalent, it has been reduced by careful control of the quality of rye used for food. Ergot also attacks ryegrass, and is a cause of abortion in cattle. On account of its medicinal value, ergot has been cultivated, by artificially infecting rye with the spores; but since the effective substance it contains is quite easily synthesized, and indeed can be improved on by other artificial products, this industry is not likely to be important in the future.

CHAPTER XVI

CLASSIFICATION

WE have now completed our survey of the more important ways in which fungi affect human life, and have given a rough idea of the structure and behaviour of a few selected types. The reader will not have gathered at all an adequate idea of the variety of the fungus world from these pages, because the majority of fungi are not, as far as we yet know, either friends or foes to any significant extent. That applies to all kinds of living organisms, of course; but it is not a sufficient reason for paying no attention to them, and the scientific study of fungi has to include *all* kinds, and cannot stop from investigating any particular type on the grounds that it is of no use, or even of no interest. A few years ago *Penicillium notatum* was a name in a monograph, of no known importance to man and, as a very typical species of a thoroughly well-known genus, of very little interest even to the specialist; today it is one of the most important of all fungi. And we never can tell when some other uninteresting item in a catalogue may not prove to be equally valuable or correspondingly destructive.

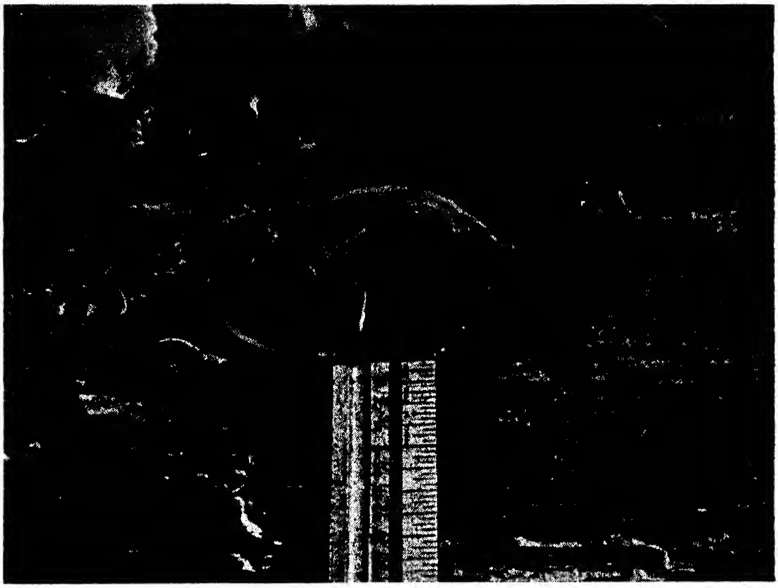
To be ready for such situations all the biological sciences have had recourse to classifications; the object of which is to enable the biologist to identify a given specimen as a member of a known species, or (occasionally) to satisfy himself and others that it represents a hitherto unknown one. Classification was the first task undertaken by biology, as by other sciences, because without it little progress could be made in any direction, and this was its original object. It has acquired however two secondary objects, which are today of a good deal of importance. These are (i) to attempt

to represent the evolutionary lines of descent of the different lines described, and (ii) to help the expert to remember the outlines of his subject. It is generally held that all three objects can be attained by a single system, but to judge by the variety of systems proposed even for the better known groups this is perhaps more difficult than it might appear. In particular for a group like the fungi, of which no reliable fossils exist, it is more or less guesswork trying to reconstruct their evolutionary history, and many mycologists discount (i) as a legitimate object in compiling a system of classification. In what follows I shall not try to explain the controversies on the subject, but shall try to outline what is generally agreed.

The fungi as a whole are sometimes regarded as algae which have lost their chlorophyll in consequence of their parasitic habits; but in view of the uniformity among the most diverse types in the structure of their cells, and their differences from both plants and animals, it is more natural (not necessarily more in accord with their actual descent) to count them as an independent "kingdom" parallel with these two major groups. For this reason the principal groups of fungi are here called phyla, which name is given to the chief groups of animals and plants, but many authorities prefer to call them classes; but of course all distinctions of this kind are quite arbitrary. Four of these phyla are generally recognised, namely the Myxomycetes, the Phycomycetes, the Ascomycetes and the Basidiomycetes. In this book we have almost confined our attention to the last two, called the "higher" fungi, because the "lower" fungi have less economic importance; but in point of biological interest, they must be counted very high, especially the Myxomycetes, on account of their wide divergence from the usual modes of structure of living bodies. Many authorities do not count the Myxomycetes as fungi; but they certainly cannot be fitted better into either of the other two chief groups of

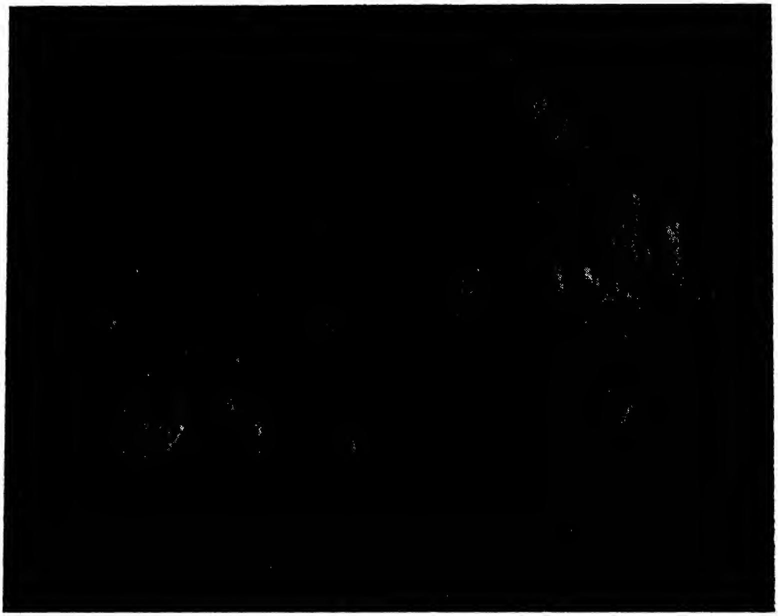
organisms. There is a fifth phylum, the Oomycetes, often included in the Phycomycetes, to which the potato blight fungus belongs. There is good ground for believing that these really are algae which have lost their chlorophyll, and if so they are quite unrelated to the other fungi, but it would be very confusing to treat them in a separate book, so that the practical thing to do is to count them as fungi, and not to pretend that classification can in this case reflect the true descent of the organisms described.

We have already described a number of Basidiomycetes; let us consider the outlines of their classification. The phylum is divided into three classes, called Hemibasidii, Heterobasidii, and Homobasidii. The first, often counted as a subphylum to emphasize its distinctness, contains chiefly the fungi causing the "smut" diseases of cereals and other crops; they have very imperfectly developed basidia, and the basidiospores are usually formed on separate cells budded off from the so-called basidium, and indeed the "basidium" may grow into a hypha without forming spores at all. Some of these have a regular phase of budding growth, in which they resemble yeasts, and there is a family of "basidial yeasts" called Sporobolomycetacei which are only found in this form, though most of them can still produce basiodiospores. The Heterobasidii are distinguished by having the basidium divided into several cells, or partly divided, or branched, and in most cases the basidiospores can bud in a yeast-like manner if conditions are not quite right for "normal" germination. There are two subclasses, called Uredinei, which are the rusts, and Tremellinei which are the non-parasitic division of the class. Most of the latter are large enough to identify without a microscope, and are very commonly of a very gelatinous consistency. The common Jew's Ear fungus (fig. 42) is a good example. The third class, Homobasidii, have basidia more or less similar to those described in Chapter I for the toadstools, and are seldom



42. EXAMPLE OF THE TREMELLINEI
Hirneola auricula-judae.

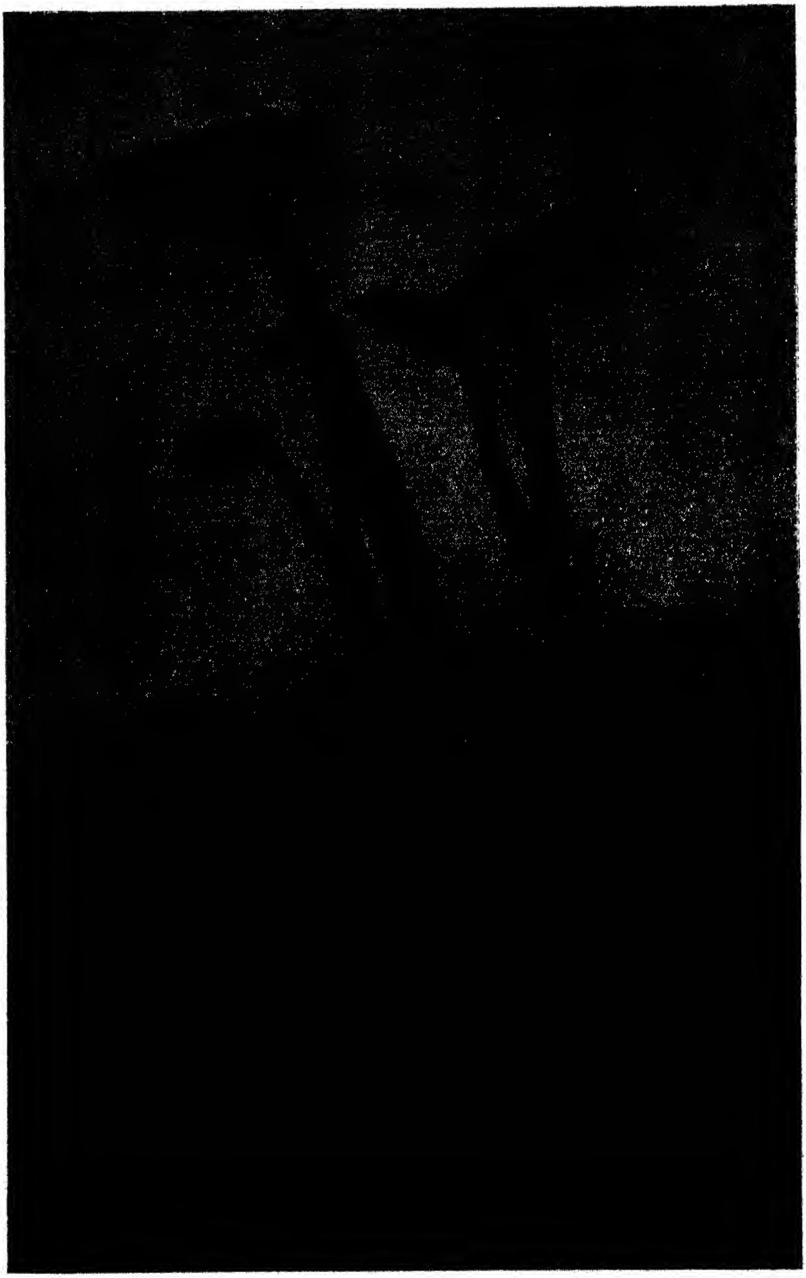
truly gelatinous; they comprise three subclasses, namely the Aphyllophori (fig. 43, p. 114), of which the woody bracket shaped fungi like *Polyporus* are the most familiar examples, the Agaricinei (fig. 44, p. 116) or true toadstools, and the Gasteromycetes (fig. 45, p. 118) including the puffballs, stinkhorns (also fig. 46, p. 121), and a great variety of other families in which the spores are produced in the interior of the fungus instead of freely exposed as on the gills of a mushroom. Because of this habit the sterigmata, whose office is to throw off the basidiospores with enough force to clear the gills, have become useless, and many Gasteromycetes accordingly have basidia without sterigmata. Some Gasteromycetes are very closely related to the toadstools, and the boundaries of the subclasses depend on how much weight the writer gives to descent as against convenience, though nearly all Gasteromycetes are probably descended from



43. EXAMPLES OF THE APHYLLOPHORI
above *a.* primitive type, *Clavulina grisea.*
opposite *b.* advanced type, *Dentinum auriscalpium*, resembling a toadstool in shape, but with spines instead of gills.

Agaricinei if we trace them back far enough. In many books the Agaricinei and Aphyllophori (and sometimes the Tremellinei as well) are included under the name Hymenomycetes.

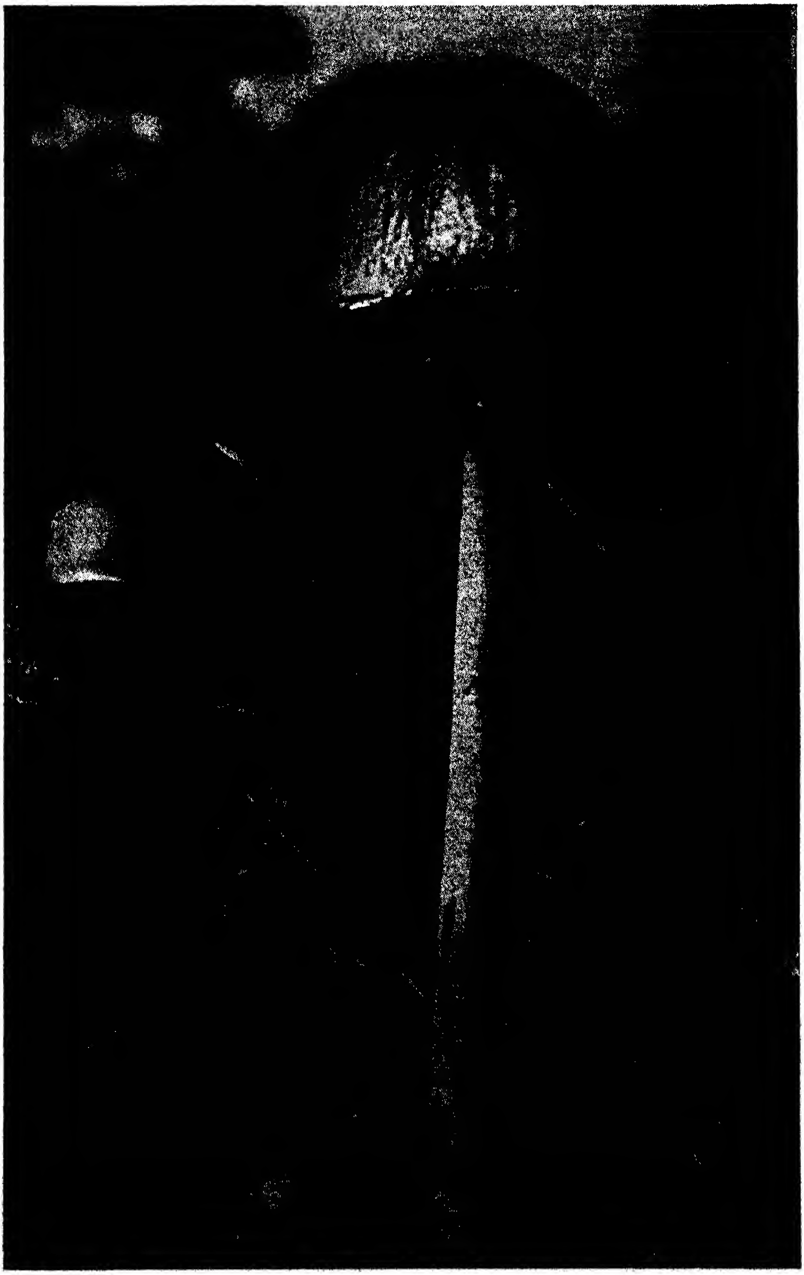
The classification of the Ascomycetes is at present in a state of flux, even more than that of the Basidiomycetes. Quite apart from the fact that a large number of them have lost the power to produce asci, on which the classification of the rest depends, and therefore cannot be fitted in, there is much evidence that there has been a great deal of convergent evolution, similar types being descended from dissimilar ancestors. Most authorities would agree to the four classes Hemiascomycetes (which have no bi-nucleate hyphae



44. EXAMPLES OF THE AGARICINEI
above *a.* primitive type, *Gomphidius viscidus.*
opposite *b.* advanced type, *Anellaria semiovata,* growing on dung.
Photo. Peter Ray.

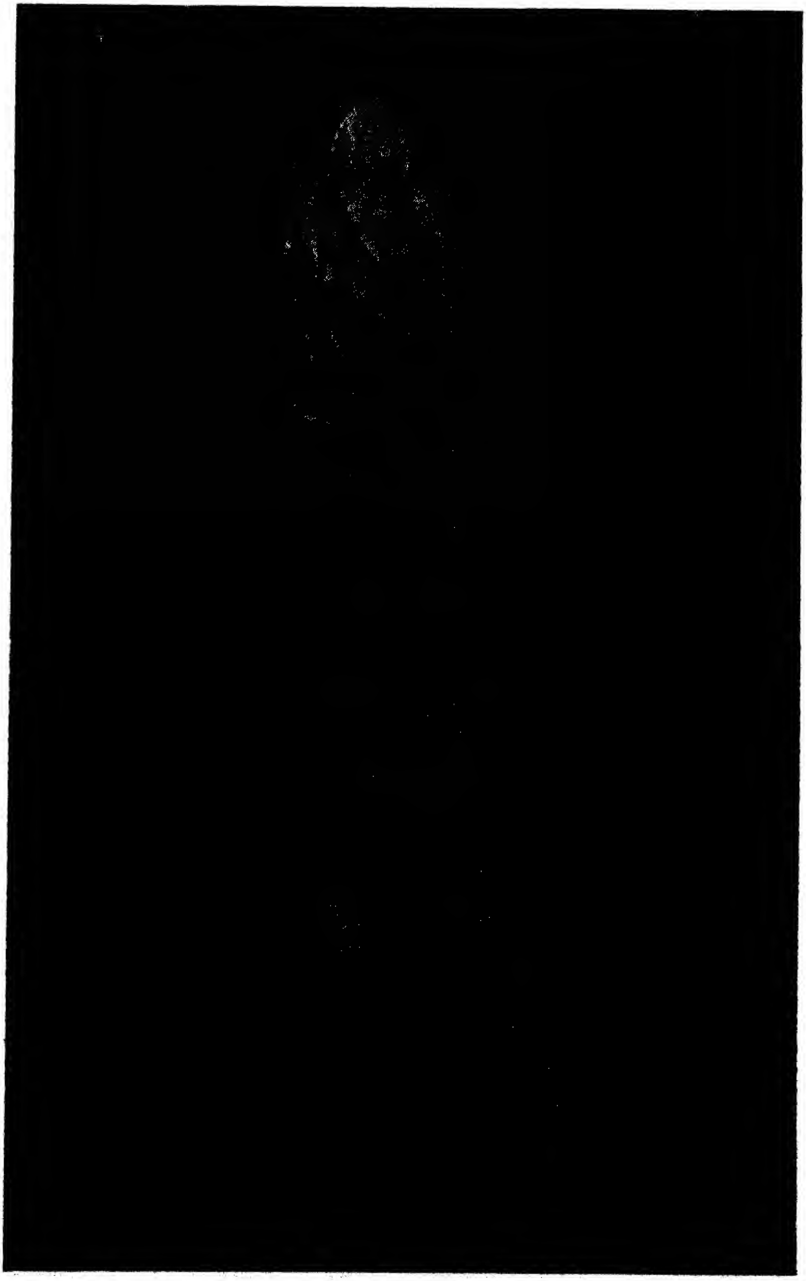
at all and include the yeasts), Discomycetes (which have asci produced on special "ascogenous" hyphae which are binucleate, like the ordinary hyphae of a typical toadstool, and exposed to the air), Pyrenomycetes (in which the asci and ascogenous hyphae are enclosed in little bottle-shaped vessels called perithecia) and Epizoomycetes or Laboulbeniales, which are very specialized fungi living on the backs of insects, but are not parasitic. Some combine the last two, and others would split up the Pyrenomycetes. The further division of these classes depends on microscopic characters, and will not be pursued here. The lichens belong mostly to various orders in the Discomycetes, but a few belong to the first and third classes also.

The Phycomycetes are fungi which form their "perfect" spores, that is those which follow upon the fusion of nuclei,



45. EXAMPLES OF THE GASTEROMYCETES
above a. Geaster fimbriatus. Photo. Mustograph.
opposite b. Phallus impudicus.

in closed bags which differ, however, from asci in that the whole of the substance is used up in spore formation, and the number of spores is indefinite; no provision is made except in a few specialized forms for the spores to be dispersed, as is done in Ascomycetes by the bursting of the ascus. The hyphae of the Phycomycetes, except those destined to form spores, have no cross-walls. The actual fusion of nuclei in most forms leads first to the formation of a special resting organ called a "zygospore" which only ger-




B
A

46. DEVELOPMENT OF THE HIGHER FUNGI

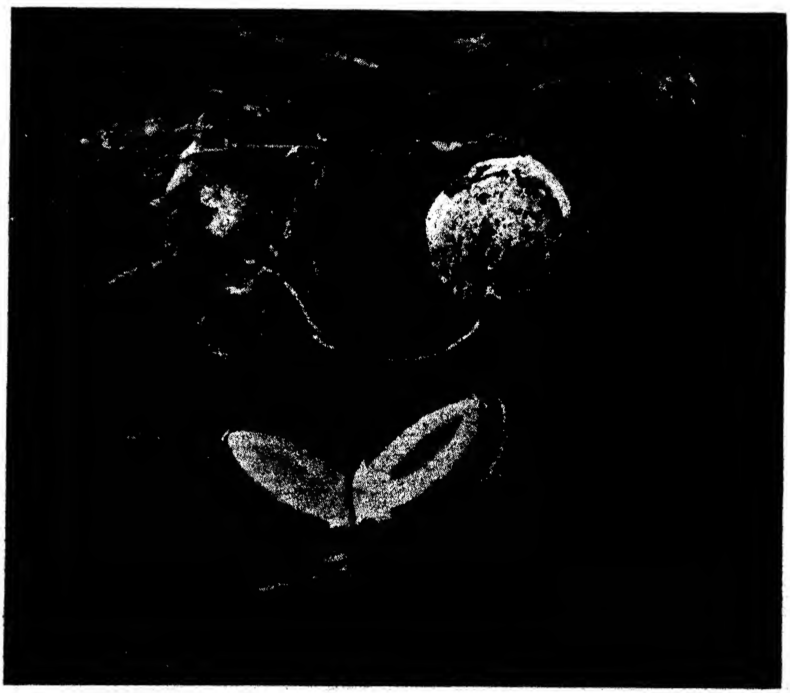
opposite top a. Various stages of a very primitive agaric, *Cantharellus infundibuliformis.* There is no covering for the very young young as seen at A.

opposite bottom b. A fairly complicated agaric, *Volvaria speciosa*, which is contained in a "volva" (like the stinkhorn "egg") when young, the remains of which are seen at A. At B is a partly opened "egg" and there is a still younger stage at the bottom of the pictures.

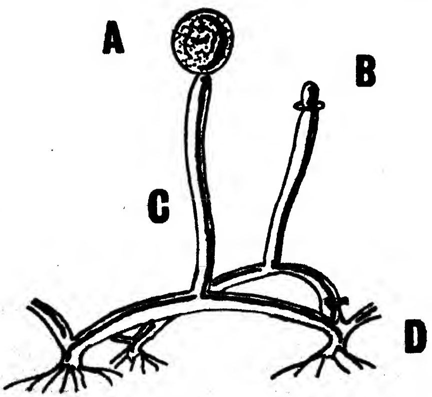
right c. Two stages of the very specialized Gasteromycete, *Mutinus caninus* (only 10 hrs between them!). This species is closely related to *Phallus.*

below d. the "egg" stage of *Phallus impudicus* (see fig 45 b) cut "stinkhorn" inside.

Photo. Mustograph.



minates to produce a sporangium after a period of maturation. In some forms the sporangium is very reduced, and may contain a single spore only, and indeed functions as a single spore, from which it can only be distinguished by its being derived from a fusion of nuclei, though in many cases this is not certainly known and we have to argue by analogy. Often reduced and typical sporangia are formed by the same fungus, just as asci and conidia are by some Ascomycetes, and it is certain that some types can produce otherwise typical sporangia *without* a nuclear fusion. This phylum contains three classes: the Archimycetes, believed by some to contain the nearest of all living fungi to the ancestral type, the Zygomycetes which is the largest part of the phylum, and the Protomycetes containing only a single genus of unimportant plant parasites, sometimes counted in the Hemiascomycetes. Many Archimycetes are true unicellular fungi, and have no hypae; their favourite mode of life is as parasites in freshwater algae, but a few cause important plant diseases, such as the wart disease of potatoes. The Zygomycetes, characterized by having zygospores (in most cases), comprise two chief orders, the Mucorales which are the common grey moulds which grow for example on jam, and can be distinguished under a hand lens by their large glossy-looking hyphae (see fig. 47); and



47. GENERAL VIEW OF RHIZOPUS NIGRICANS
a representative of the Zygomycetes.

A. ripe sporangium, containing numerous spores.
B. remains of sporangium which has discharged its spores; this is aided in this genus by swell- of the columella which you see here at the tip of the sporangiophore.
C. sporangiophores and horizontal hyphae called "stolons".
D. rhizoids, or special narrow hyphae which act as "roots".

the Entomophthorales, most of which are parasites on insects, and cause a fatal disease of flies, as a result of which they become stuck to the surface they walk on and presently become covered with the spores of the fungus. It is believed by some that this may be one of the major factors restricting the population of flies, and if so these fungi are of great economic importance to mankind.

An interesting characteristic of many of the lower Phycomycetes is that they reproduce by zoospores, like those of the potato-blight fungus, except that they have only one swimming "tail" instead of the two which are characteristic of the Oomycetes. In a few forms the nuclei, which will initiate the formation of the sporangium, are brought together by the fusion of two of these zoospores, while in an aquatic genus called *Monoblepharis* this is done by a zoospore attaching itself to a large stationary cell, just like a spermatozoon and an egg-cell among higher plants and animals; this is about as far as any fungi have got in the direction of evolving two sexes, if we except the Oomycetes, and represents a side-line in their development, which as far as we can see was never followed up.

The Myxomycetes comprise several classes, the true relationship of which to each other is very dubious; of most of them very little is known. One genus *Labyrinthula* (described here for no better reason than that every classification has to have a "miscellaneous" category) is of considerable importance because it causes a disease of the zostera-grass which is used to aid in the reclamation of land from the sea; since it grows below low-water mark and its roots bind the shifting sands, the disease is very serious on the coasts of Holland and parts of England; *Labyrinthula* is practically the only example of a fungus (if it is one) which lives in the sea. The chief class of Myxomycetes which we shall mention is the Mycetozoa (including the great majority of species of the phylum). The life history

of one of these begins with a zoospore; on reaching a suitable habitat it draws in its single "tail" (it is very like the zoospore of a Phycomycete) and begins to creep about like an amoeba; it prefers usually rotten wood or soil. Like an amoeba it can envelop and then digest any suitable food particles, but it can also absorb nutriment through its general surface. If it meets with another of its kind, it will move up to it, and the two will flow together; thus far it might be a Phycomycete, some of which have amoeba-like stages; but after one fusion the nuclei do not join together but rather continue to divide independently, and the first may be followed by a whole series of other fusions, until, partly by its own growth and partly by absorbing others of a like kind, the amoeboid mass, which is called a plasmodium, may attain a diameter of several inches, though it remains very thin. All this time it continues to move and to feed, and furthermore is able to respond to its environment, both by seeking food put near it and by retreating from the light. At length however it changes its mind about this and creeps out into an exposed situation, where a very remarkable development takes place; at various points the protoplasm gathers itself together into little heaps, and each heap begins to grow into a sporangium, in which (it is said) every nucleus in the neighbourhood of the heap is at length packed into a spore. Probably the nuclei fuse in pairs before this happens. Each spore on germination liberates four zoospores. The stage of the Mycetozoa most familiar to most people is the sporangia, which are formed in dense crowds covering several square inches of a rotten log or stump; each sporangium is usually more or less drumstick-shaped, and may be up to $\frac{1}{4}''$ high, and they are often brightly coloured. Same species of *Lycogala* may reach a diameter of an inch or more and their sporangia look like small orange or grey puff-balls.

A third class of Myxomycetes is that of the Phyto-

48. TWO VERY DIFFERENT STAGES IN THE LIFE OF AN AGARIC A species of *Coprinus* growing from a mass of brown fibres, which is called *Ozonium* because it used to be thought a different kind of fungus altogether.

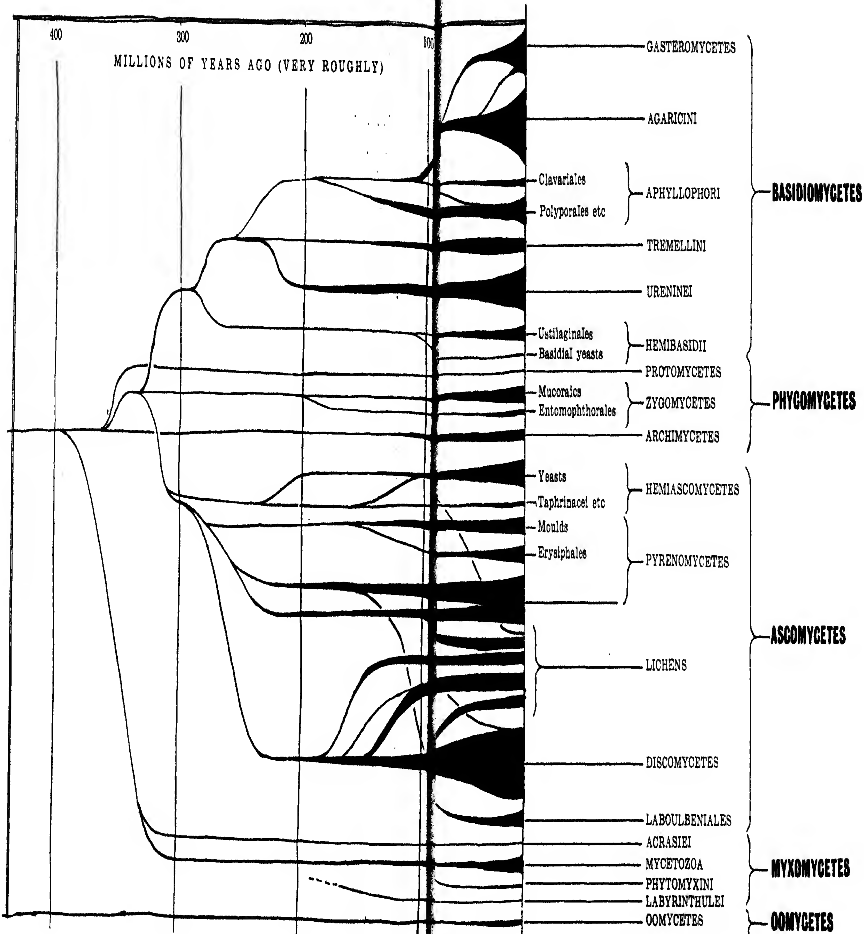
myxini; these differ from the Mycetozoa in being parasites in plants, and there are a few serious diseases caused by them, one of the best known being the "finger-and-toe" of cabbages, so called because of the malformation of the roots which is its most obvious symptom. The life history given above for the Mycetozoa hardly applies to the Phytomyxini, whose mode of life inside the tissues of a plant has induced a good deal of modification; however they too form plasmodia and sporangia.

This brings us to the end of a very summary sketch of the classification of fungi, and it will have been realized that for those with a taste for classification there is a vast field of uncertainty waiting to be broken by research. This uncertainty becomes more pronounced at the lower levels of the hierarchy; we have mentioned classes and subclasses, and below these according to the commonest convention are orders, families, tribes, and genera, and at each level there is more room for dispute about relationships, quite apart from the really unnecessary controversies between those who seek to represent evolutionary lines and those who prefer artificial but more utilitarian schemes of classification. The best solution is probably to have on the one hand an evolutionary system (which is useful at least by helping the student to keep in mind the greatest number of relevant facts about each group) and on the other an artificial key for the purpose of identifying an unknown specimen. Classification is one of the few branches of science which is even now better undertaken by one man than by a team, and it is possible that a sufficiently diligent student who made it his life-work could clear up most of the problems at the purely classificatory level. There are about 70,000 species of fungi many times more than all the plants and animals arranged by Linnaeus, but allowing for the greater knowledge we now have about these species than Linnaeus had about his, the tasks are comparable in magnitude.

EPILOGUE

THE important thing, which it is hoped that the reader will have learnt from these pages, is that like all other sciences that of the study of fungi is continually in a state of expansion. Time and again we have had to conclude our brief remarks on some topic by saying that very little is known about it; and where this is not said, it should be assumed that we have not yet advanced far enough to realize that this is so.

The most obvious gaps in our knowledge concern the many diseases of crops caused by fungi which are little known and less understood; but these are the gaps which in time will be filled in any case, if enough money is devoted to it, because they promise an immediate return. But equally desirable is an understanding of such topics as how the developing fungus regulates its form, so as to give rise to its characteristic adult appearance, especially in the case of the Mycetozoa. This knowledge is not required merely to satisfy curiosity but because, to judge by past experience, an understanding of these things will be found helpful and useful in all kinds of unexpected ways, which it would be idle to try to predict. Another subject which would repay study would be the genetics and breeding of fungi, not merely to obtain better kinds of those species directly useful to man, but to find out for example whether the binucleate arrangement, unique to the Basidiomycetes among all known organisms, has any effect on the mechanism of heredity, which is fairly well understood for animals and plants. Again, the evolution of the fungi is practically a closed book (despite fig. 49), though perhaps a very hard one to open, let alone to read. These are a small selection of the problems awaiting elucidation, to solve one of which is to raise a dozen more. For indeed science has no end.



49. DIAGRAMMATIC VIEW OF THE EVOLUTION OF THE FUNGI

This diagram is intended to show only one of many hypotheses about the relationships of the different groups; the width of the branches at the top gives a rough idea of the biological importance of the various groups today, but it is *not* intended to suggest anything about their position in the past. The time scale is largely based on conjecture from the known relationship of the various groups to the higher plants, whose history is known from fossils. It must not be taken very literally.

FOR FURTHER READING

THERE are few good popular books on the fungi; the best of those which do not aim to help in identification is *The Advance of the Fungi* by E. C. Large (London, 1940).

For those who wish to eat fungi, it is inadvisable to rely either on written descriptions or on illustrations, unless they are well trained in their interpretation; the best guide for this purpose is given in two booklets entitled "Edible Fungi" and "Poisonous Fungi" by J. Ramsbottom (King Penguin Books).

For identification of the species which do not need a microscope for their study, I recommend J. Ramsbottom's "Handbook of the Larger British Fungi" (British Museum Trustees, 1923). The standard work on the Basidiomycetes is Carleton Rea's "British Basidiomycetae" (Camb. Univ. Press, 1922), but it has no illustrations. For the identification of Lichens the standard work is Lorraine Smith's "British Lichens" (Routledge). For other groups of fungi special monographs have to be consulted, which are of little use except to experts; in any case, you should not assume that you will be able to indentify a fungus correctly from the above books without considerable practice.

Among a variety of textbooks on the scientific study of fungi, we may cite Gwynne-Vaughan and Barnes' "The Structure and Development of the Fungi" (Cambridge Univ. Press, 1937).

A diffuse but readable book on various aspects of fungus life including a certain amount on the history of the subject is "The Romance of the Fungus World" by R. T. and F. W. Rolfe (Chapman and Hall, 1937). The literature on plant diseases and their treatment is very extensive, and is beyond the scope of this brief guide; any person may obtain free information and advice on specific problems from the

Mycological Advisory Service of the Ministry of Agriculture, situated usually in the nearest university town.

For a general account of the industrial applications of mycology, read "Industrial Mycology" by G. Smith (Arnold 1946).

GLOSSARY

Aecidiospore a spore having two nuclei, produced by rust fungi on their spring hosts, which infects the summer host with the binucleate mycelium.

Aecidium the sorus in which aecidiospores are produced.

* *Apothecium* a form of ascocarp in which the hymenium is exposed as a flat layer when mature.

Ascocarp the body, distinct from the mycelium, in which most Ascomycetes produce their asci; it is the visible part of the fungus.

Ascogenous hyphae special hyphae found in the ascocarp, whose function is to bear the asci; they are distinguished from the rest in being binucleate, and are the only binucleate hyphae in Ascomycetes.

Ascospore the type of spore produced in an ascus.

Ascus the cell of an Ascomycete in which the fusion nucleus divides to produce the perfect spores; usually the zeugite. Pl. *asu.*

Basidiospore the type of spore produced on a basidium.

Basidium the cell of a Basidiomycete in which the fusion nucleus divides to produce the perfect spores; in the larger forms it is also the zeugite. Pl. *basidia.*

Binucleate having in every cell two nuclei, which divide always together.

* *Cap* synonym for pileus, used in some books on fungi.

Cell in fungi the term cell is commonly applied to the part of a hypha between two of the cross-walls which divide it; a more general definition is a portion of cytoplasm furnished with one or more nuclei.

Chlamydospore an imperfect spore produced by simple modification of one of the cells of the mycelium, having a thick wall and able to resist unfavourable circumstances.

* *Conidiophore* special hypha bearing conidia.

Conidium any thin-walled imperfect spore. Includes oidia and some microspores as special cases. Pl. *conidia.*

* *Cortina* that part of a toadstool which encloses the pileus and stem or protects the gills when young; sometimes seen in the mature form as a ring round the stem, or as fragments hanging from the edge of the pileus.

* *Dicaryon* a pair of nuclei which divide together in a binucleate cell.

* *Diploid* having cells in which there are two sets of genes; in fungi this means having two nuclei (except the zeugites, and perhaps the ordinary cells of some yeasts).

Diploidization the process, in Basidiomycetes, whereby a uninucleate mycelium becomes binucleate on meeting another mycelium suitably related to it.

* *Ectotrophic* term applied to that type of mycorrhizon in which the hyphae do not penetrate into the cells of the plant.

* *Endotrophic* having hyphae which do penetrate the cells of the plant. Opposite of ectotrophic.

Genes the ultra-microscopic bodies contained in the nucleus of every cell of an organism, which cause the inheritable characters of the organism to be produced in the course of its growth.

Genus a group of related species considered to form a genus by a competent taxonomist. Pl. *genera*. In the Latin name of a species the first word is the name of the genus (always written with a capital letter) and the second distinguishes the species (has a capital only if derived from the name of a person).

Germ-tube the hypha first formed by a germinating spore; it is usually narrower than the ordinary hyphae, and has no cross-walls.

Gills the radiating plates seen underneath the pileus in most toadstools, on which the spores are borne.

* *Haploid* possessing only one complete set of genes in the cells; opposed to diploid. In fungi it is almost synonymous with uninucleate.

Haustorium an organ of certain parasitic fungi, especially rusts and mildews, which serves to extract their food out of the hosts cells. Pl. *haustoria*.

Heteroecious a term describing those rusts which require two different hosts to pass their full life-cycle.

* *Heterothallic* possessing two or more strains or "sexes", which have to be combined (in certain pairs only) in order that successful formation of the perfect spores should ensue.

* *Hymenium* a special surface layer, in toadstools and various various other fungi, composed of the spore-bearing cells; found for example on the gills of toadstools or lining the apothecia of lichens.

Hypha one of the threads forming the mycelium. Pl. *hyphae.*

* *Hypnospore* a name for any kind of spore adapted to withstand a prolonged period of unfavourable conditions, usually being unable to germinate until after many months of maturation. Includes oo-, zygo-, and some kinds of chlamydo-spores.

Imperfect a term applied to those spores of a fungus which are formed without any fusion of nuclei.

* *Lamella* synonym for gill. Pl. *lamellae.*

* *Microspore* a name for any kind of spore distinguished for unusually small size; typically they consist of little besides a nucleus, and in some cases serve for purposes of diploidization. Includes the spermatia of rusts.

Mycelium includes all the hyphae of a fungus other than those which make up the spore-bearing structure, such as the visible toadstool or bracket. Mushroom-growers call it "spawn".

Mycology the scientific study of fungi.

Mycorrhizon a root or other part of a plant associated with a fungus, in such fashion that neither can be shown to be parasitic on the other but exist in symbiosis. Pl. *mycorrhiza.*

Nucleus a special body existing in all living cells, essential to the life of the cell, and carrying the genes which determine the characters of the organism. Pl. *nuclei.*

Oidium a special sort of conidium produced in long chains; especially applied to the imperfect spores of mildews. Pl. *oidia.*

Oospore the zeugite and (usually) hypnospore of the Oomycetes, formed by union of organs which can be distinguished as male and female.

* *Paraphysis* one of the special hypae which are packed side by side with the asci in the ascocarp of Ascomycetes; they are believed to help in the bursting of the asci. Pl. *paraphyses.*

Parasite any organism which draws part or all of its food from another living organism, called its host.

Perfect term applied to those spores of fungi which are produced as the result of a fusion of nuclei.

Peridium the outer skin of a puffball. Pl. *peridia.*

* *Perithecium* an ascocarp in which the asci are contained in a globular or flask-shaped vessel having a hole or ostole at the top; often incorrectly applied to the ascocarps of mildews, which have no ostiole. Pl. *perithecia.*

Phylum the largest group of organisms commonly used in classification; it has no precise definition, like all classificatory terms. Pl. *phyla.*

Pileus the expanded upper portion of a toadstool which carries the gills or tubes. Sometimes applied to the bracket of the Aphyllophori. Pl. *pilei.*

* *Probasidium* a zeugite from which the basidium grows in certain basidiomycetes. Includes the teleutospores of rusts.

Protoplasm the name given to the substance, other than cell-wall material or the watery solution found in some cells, of which living organisms are composed.

Rhizomorph a specially modified type of mycelium possessed by some fungi such as the honey-fungus, consisting of long strands having a hard and often dark coloured outer crust.

Saprophyte an organism which, while not depending on *living* organisms for its food as parasites do, requires to take its food from the dead remains of other organisms by a process of passive absorption; contrasted with plants which can make their own food.

Sclerotium a hard and compact body formed by the mycelium of certain fungi, and able to withstand unfavourable periods; differs from a hypnospore in being large and made up of many hyphae.

Sorus a bunch or patch of spores produced by aparasitic fungus on its host plant, especially used of the rusts. Pl. *sori.*

Species a group of organisms sufficiently alike to be considered worthy of a specific name by a competent taxonomist. See genus. Pl. *species.*

Spermatium a microspore borne by the uninucleate mycelium of certain fungi, especially rusts. Pl. *spermatia.*

* *Sporangiophore* special hypha bearing a sporangium.

* *Sporangiospore* a spore produced in a sporangium.

Sporangium any cell or vessel in which spores are produced, but especially the perfect spore-bearing organ of the Phycomycetes and Mycetozoa. Pl. *sporangia.*

Spore a reproductive body not containing an embryo but capable of growing into an adult form without fertilization. In the case fungi the term is applied to some bodies, such as hypnospores, which do not aid in the dispersal of the species from place to place, but merely perpetuate it.

* *Sporidium* a small spore formed by budding of the basidiospores of certain species (such as Dacryomyces, fig. 7). Applied in some books to the basidiospores themselves. Pl. *sporidia.*

* *Sterigma* the minute stalk on the apex or side of the basidium on which the spores are borne; also applied to the finest branches of the spore-bearing hyphae of the Aspergillacei (Fig. 19 c) Pl. *sterigmata.*

* *Stipe* synonym for the stem of a fungus.

* *Symbiont* one of two or more organisms living in symbiosis.

Symbiosis the habit of two or more organisms which can live only in association with one another, or live better so, in which neither can be said to be parasitic on the other.

Tube one of the cavities found in place of gills under the pileus of certain toadstools (viz: the Boletacei), which are lined by the hymenium.

Teleutosorus the sorus in which teleutospores are borne.

Teleutospore the zeugite and hypnospore of the rusts.

Uninucleate possessing only one nucleus in each cell of the

Uredosorus a sorus containing uredospores.

Uredospore a spore possessing two nuclei formed by a rust fungus on its summer host to perpetuate the binucleate mycelium.

Veil the cortina; the part enclosing the whole toadstool is called the *universal* veil, and the part covering the gills, which remains behind in the adult state as a ring, is the *partial* veil.

Volva the remains of the universal veil forming a cup at the base of the stem; the term is also applied to the peridium of the stinkhorn fungi (Phallacei).

* *Zeugite* a special cell of the binucleate mycelium in which the two nuclei fuse together, preparatory to forming the perfect spores.

Zoosporangium a sporangium containing zoospores.

Zoospore a reproductive body consisting of a single cell with a nucleus, furnished with a fine tail or swimming hair by means of which it can swim through water; produced by the lowest fungi only.

Zygospore the zeugite (nearly always also a hypnospore) of the Zygomycetes, formed by the union of organs not distinguishable as male and female.

Terms marked * are not used in the next, but are included in the Glossary for completeness.

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